INVESTIGATIONS OF PATTERNS OF VEGETATION, DISTRIBUTION AND ABUNDANCE OF SMALL MAMMALS AND NESTING BIRDS, AND BEHAVIORAL ECOLOGY OF ARCTIC FOXES AT DEMARCATION BAY, ALASKA

A
THESIS

MASTER OF SCIENCE

By
Robert M. Burgess, B.A..

Fairbanks, Alaska
May, 1984

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AT DEMARCATION BAY, ALASKA

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Presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
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ABSTRACT

Analyses of habitat use, activity budget and activity patterns of arctic foxes (Alopex lagopus) at known distribution and abundance of prey are presented. Behavioral data on foxes were collected by direct observation of 2 radio-collared females and their mates in summer 1979. Prey availability was determined through monitoring bird nest success and phenology, mark-recapture studies of small mammals, and analysis of vegetation patterns and distribution of prey in 1978 and 1979. Prey availability fluctuated dramatically within each season and between years. Foxes relied almost exclusively on avian prey in 1979. Small mammal densities were extremely low in 1979 and foxes failed to rear pups in that year. Fluctuating prey availability did not affect fox activity patterns, activity budget or habitat use. The significance of caching in regulating food availability and the relationship between scent-marking and foraging efficiency are discussed.

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INTRODUCTION

The arctic fox (Alopex lagopus) is a small canid highly adapted to arctic conditions. Special features of morphology, physiology, reproduction and behavior make the arctic fox one of the most highly adapted of arctic animals (Scholander et al. 1950). Perhaps the primary adaptation is the insulative quality of its dense winter fur. The thick winter pelage provides extreme cold tolerance. The lower critical temperature in winter is below -35° C, in summer it is between 0° C and -10° C (Underwood 1971). The fox is, therefore, more likely to encounter conditions exceeding the lower critical temperature in summer than in winter.

Investigations of arctic fox ecology have been conducted in several areas of its circumpolar distribution. These include Greenland (Braestrup 1941, Vibe 1967), Baffin Bay (Elton 1949), Keewatin and Franklin Districts, Northwest Territories (Macpherson 1969, Speller 1972), near Prudhoe Bay and the Colville River (Underwood 1975, Eberhardt 1977, Fine 1980, Garrott 1980, Eberhardt et al. 1982), near Barrow (Chesemore 1967), on St. Lawrence Island (Stephenson 1970), and in the USSR (Dementyeff 1958).

The range of the arctic fox is limited by the distribution of arctic tundra and interspecific competition with red foxes (Vulpes vulpes) (Chesemore 1967). In most portions of their range (exceptions are insular situations), arctic foxes have been found to move seasonally between summer breeding habitats in wet tundra and winter habitats, where they are widely dispersed on the coast and far out on

the sea ice. The initiation of fall movements has been attributed to food scarcity (Tchirkova 1958a, Dementyeff 1958, Chesemore 1967).

In all areas of the range of arctic foxes, the distinct seasonality of climate imposes seasonality in food availability and food habits of arctic foxes (Chesemore 1967, Stephenson 1970, Eberhardt 1977). Distinct regional differences in seasonal diets of continental and insular arctic foxes have been reported. In most tundra areas, microtine rodents (lemmings and/or voles) have been identified as the primary summer prey. Birds and eggs are seasonally important, at least during periods of low microtine availability. Caribou (Rangifer tarandus) and marine mammal carrion are particularly important winter foods, and in spring many arctic foxes become active predators of seal pups in lairs (Smith 1976, Riewe 1977). In a few insular situations where nesting birds and products of the sea are consistently available and competitors mostly lacking, foxes can survive without small rodents. Such foxes are almost exclusively of the blue color phase (Underwood and Mosher 1982).

In areas where arctic foxes are dependent on microtines, denning and reproductive success are related to oscillations in microtine abundance (Speller 1972). Low lemming density may delay estrous and increase pre- and post-natal mortality through abortion or resorption (Tchirkova 1958b, Macpherson 1969, Speller 1972).

Arctic foxes are monogamous and the male of a pair takes an active role in supporting the post-partem female and in pup-rearing. A strong pair bond is apparently required by the inability of a single

adult to feed the large litters of pups in most situations (Speller 1972). Average litter size from embryo and placental scar counts is 10.6 (Macpherson 1969). Arctic fox vixens are monestrous, with estrus lasting 12 to 14 days. Breeding takes place usually in March or April, but with much regional and individual variation attributed to such factors as nutritional state of the fox, ambient temperature and photoperiod. Gestation lasts 52 days and the pups are usually born in an underground den. Dens are described by Garrott (1980).

Pups disperse from natal dens in late summer. In years of food abundance, adults may remain at breeding sites well into winter. In years of low food abundance, adults may abandon the den site before pups have dispersed. Many instances of sporadic and long-distance movements have been noted (Chesemore 1968a, Northcott 1975, Wrigley and Hatch 1976). The best documented have been for dispersing pups (Eberhardt and Hanson 1978). The varying proportions of adults and juveniles in annual harvests have been attributed to changes in age structure of the wandering portion of the populations (Macpherson 1969).

Food requirements of the arctic fox in summer are greater than in winter. The amount of food voluntarily ingested by captive arctic foxes maintained under arctic conditions varied from 1548 kJ/kg•d in July to 264 kJ/kg•d in January (Underwood 1971). Activity levels are highest and increased energy requirements due to reproduction also occur in the summer when food is typically most abundant. Energy

requirements are, therefore, lower during the season when food abundance is most limited.

The impact of fox predation on prey populations is the subject of some controversy and appears to be quite variable locally and between years. Food consumption by an average litter of 10.6 pups averages 60 lemmings per day or 2400 lemmings over a 40-d denning season (Speller 1972). Although large numbers of microtines may be consumed by a family, foxes are not considered to regulate microtine numbers or to drive cycles in microtine abundance (see Pitelka et al. 1955; Pitelka 1957, 1973; Maher 1970; MacLean et al. 1974). Several studies have documented devastating effects on local abundance of birds, particularly in periods of low microtine availability (Mayfield 1976, Riewe 1977). The distribution of many arctic nesting birds may reflect adaptations to minimize fox predation (Bertram and Leek 1938, Larsen 1960, Speller 1969). Introduced foxes on some of the Aleutian Islands have severely reduced nesting birds. Aleutian Canada geese (Branta canadensis leucopareia), whiskered auklets (Aethia pygmaea) and Cassin's auklets (Ptychoramphus aleuticus) are particularly vulnerable.

This investigation of arctic fox ecology concentrated on the habitat use, activity budget and activity patterns of arctic foxes in the Demarcation Bay area of Alaska (Fig. 1). A simultaneous assessment of prey populations and distribution allowed relating behavioral observations to resource availability. Specific objectives were:

1) To examine food habits, activity budgets, activity patterns and habitat use at a known level of resource availability.

2) To examine social and foraging activities and elucidate the functions of individual behaviors, particularly caching and scent-marking.

3) To examine the seasonal distribution and availability of prey and its effect on arctic fox activity and habitat use.

4) To attempt to assess the impact of arctic fox predation on prey populations at a known level of overall resource abundance.

In 1978 emphasis was placed on objective 4 through intensive monitoring of prey populations within and outside an exclosed area created with electric fence. The technique proved impractical for the limited resources of a remote field site and was abandoned. Too few observations of foxes were made for an analysis of arctic fox ecology or behavior. The focus of the investigation was altered in 1979. Radio-telemetry allowed detailed observation of resource use by foxes and the effect of resource availability on foxes.

STUDY AREA

The Arctic National Wildlife Refuge (ANWR) lies in the northeastern corner of Alaska. It contains biotic communities ranging from mixed evergreen and deciduous forest on the south slope of the Brooks Range to alpine and coastal tundra and arctic estuaries on the north slope. The area is remote from human influence and typifies northern Alaskan wilderness. All major arctic communities are represented. The refuge is roadless, and is accessible by airplane, boat, snow machine, dog sled or on foot. Four major physiographic provinces are represented in the region from south to north: 1) northern plateaus, 2) arctic mountains, 3) arctic foothills, and 4) arctic coastal plain (AEIDC 1975). From May through early August daylight is continuous. The climate is dry arctic; precipitation averages 15 cm per year, mostly in the form of snow.

The refuge is the summer home of 143 species of birds; 104 are known to breed there. Twenty-two species of land mammals inhabit the northern parts of the refuge and 7 species of marine mammals are known to occur along the coast.

The study area for this investigation was located east of Demarcation Bay in the northeast corner of the ANWR, 141°15' W longitude and 69°40' N latitude. The coastal plain in this area is narrow, the foothills beginning approximately 11 km south of Demarcation Bay. Wet coastal plain is limited to areas east and west of the bay; dry tussock tundra occurs between the foothills and the south shore of the bay. The study area was confined to the wet

coastal tundra between the east shore of Demarcation Bay and Canada to the east, and the dry tussock tundra province to the south (Fig. 1).

Aside from its narrow width, the wet coastal tundra in the study area is similar to wet tundra along the Beaufort Sea coast from Prudhoe Bay to the MacKenzie River Delta. The terrain is generally flat, underlain by permafrost and exhibiting ground features caused by seasonal frost action: polygons, frost boils, thaw lakes and meadows. Low uplands of 8 to 15 m elevation are conspicuous features providing a few widely dispersed areas of well-drained soil. The study area is unique in the ANWR in possessing several large lakes with some evidence of a thaw-lake cycle similar to that described for tundra areas to the west. A large proportion of the tundra in the study area remains covered with shallow standing water throughout the summer.

Weather data collected by the National Weather Service (1978, 1979) at Barter Island (approximately 110 km west) are shown in Fig. 2. Surface winds blow nearly constantly on the coast; calm conditions were rarely recorded. Visibility is often poor due to ground fog beginning in June when open water first appears in the Beaufort Sea. Observations of wildlife were frequently hampered by heavy fog.

Intensive investigations of nesting birds, small mammals and vegetation were conducted on a 30 ha (480 m x 640 m) study plot located near the Distant Early Warning (DEW) line site which was our headquarters. This study plot was approximately 200 m from the coast

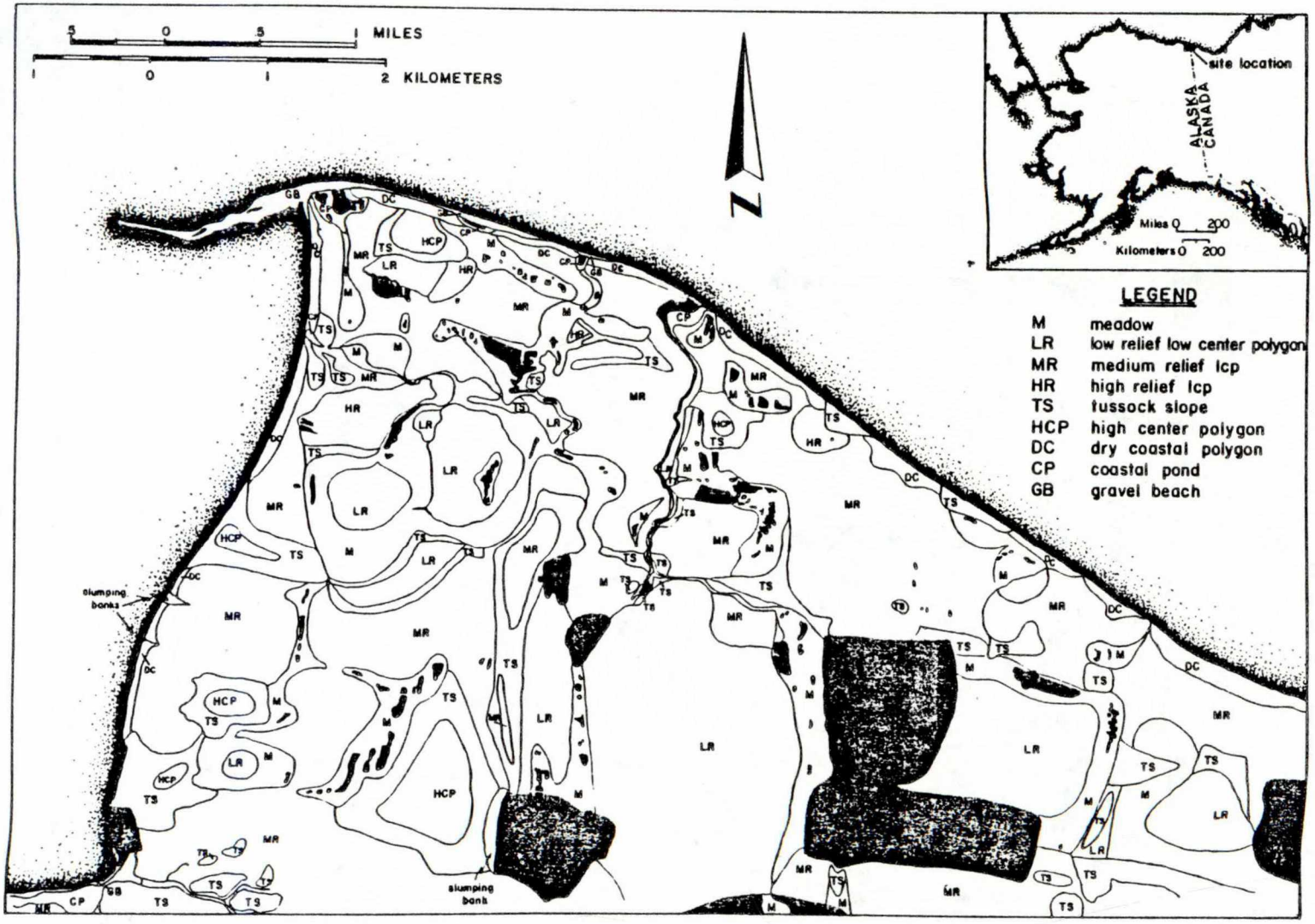

Figure 1. Location and vegetation map of arctic fox study area at Demarcation Bay, Arctic National Wildlife Refuge, Alaska.

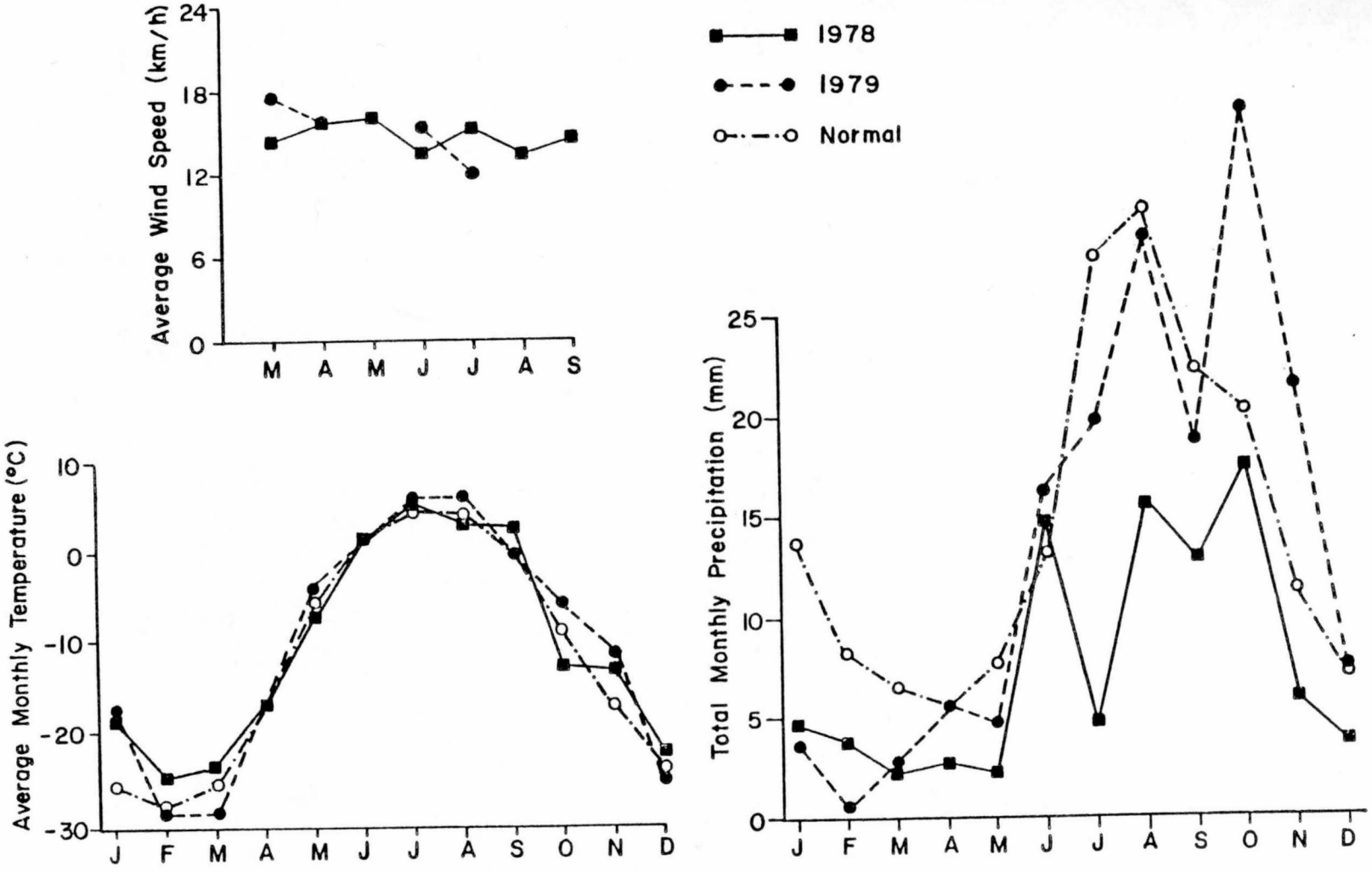

Figure 2. Climatological data from Barter Island, Alaska (from National Weather Service 1978, 1979).

of Demarcation Bay to the west and 200 m from the Beaufort Sea coast on the north, and was composed of a dense interspersion of the major tundra habitats along the south and west slopes of a coastal bluff (Fig. 3). The dry summit area of high center polygons with thermokarst troughs sloped toward the south to tussock slope and dry Carex meadow which bordered an Arctophila marsh. To the west the tussock slope had solifluction ridges with associated ponding; as the slope decreased it graded into an area of frost boils in dry Carex meadow. The west side of the study plot was a wet drainage area with a small pond, draining north through wet Carex and Dupontia meadows and into a coastal pond system of brackish water with associated salt marsh vegetation. Borders between habitats were typically abrupt.

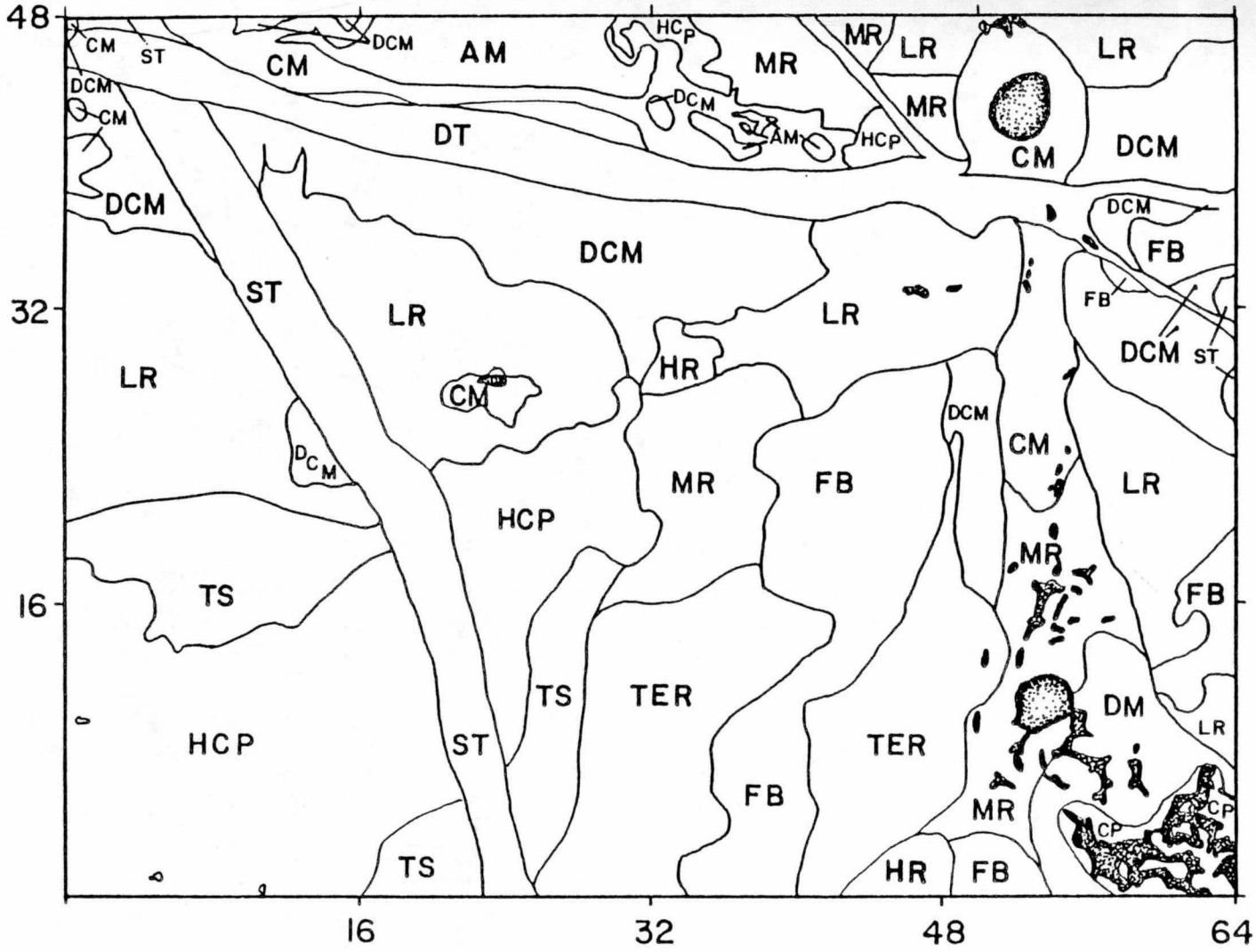

Figure 3. Vegetation map of the 30-ha study plot at Demarcation Bay, Alaska. Vegetation type codes are as defined in Table 1. Coordinates are in 10-m intervals and the divisions shown illustrate boundaries of the 12 trap areas used in the small mammal trap effort. Trap grids were centered in each 160 m x 160 m trap area.

METHODS

I. VEGETATION ANALYSIS METHODS

The 30-ha study plot was staked in a grid pattern at 10 m x 10 m intervals. Grid line intersections were chosen randomly for sampling to characterize important vegetation types. At each grid intersection sampled, the vegetation was examined on a 1 m x 1 m plot. Additional 1 m x 1 m plots were sampled at each small mammal capture location and each bird nest found. In 1979, additional samples were taken on plots placed in more extensive and homogeneous vegetation types south and east of the 30-ha study plot. These areas were also trapped for small mammals.

On each 1 m x 1 m plot the following data were collected: species of vascular plants present; percent cover of dominant vascular plant species (names are as in Hultén 1968), moss, lichen, water and bare ground (each plot had 100% cover total); and percent cover by 6 moisture regimes (flooded, wet, wet to moist, moist, moist to dry and dry). Moisture was evaluated from visual and tactile characteristics. In 1979 samples, measurements were also made of microrelief (the vertical distance between the lowest and highest elevations on the 1-m^2 plot) and the average vegetation height of the dominant species on each plot. Vegetation height was measured with a meter stick placed at 5 to 10 locations on the plot, readings being taken at the highest point at which vegetation touched the stick. The readings were averaged for a single final value of vegetation height.

Data on moisture were condensed into a single value for each plot. The moisture index was calculated by dividing percent cover values for dry by 100, values for moist to dry by 50, moist by 33.33, moist to wet by 25, wet by 20 and flooded by 16.67, and then summing values for each category. This yielded an index ranging from 1 (dry) to 6 (flooded), reflecting proportionate cover by the 6 moisture regimes.

A detailed vegetation/landform map of the 30-ha study plot was prepared by combining 12 field-drawn maps of 160 m x 160 m portions. Each 1-m^2 sampling plot was subjectively assigned to a vegetation/landform type through examination of cover characteristics, physical parameters and location on the map. On the 30-ha study plot, 15 distinct vegetation types were recognized based on vegetation patterns and micro-relief features (Table 1).

A vegetation map of the entire study area was prepared from high altitude aerial photos and modified throughout the study by ground truthing. The end result is a detailed vegetation map recognizing 11 major types, 3 of which were not found on the 30-ha plot (Table 1). The increased focus on the study plot allowed some major vegetation types to be logically divided into ecologically distinct but physiognomically similar types, thereby accounting for the larger number of vegetation types recognized on the 30-ha plot. In addition, the proximity of the 30-ha plot to a former DEW line station overemphasized the extent of habitats physically altered by man: 2

Table 1. Area and percent coverage of vegetation types recognized on the 30-ha plot and their equivalents mapped from high altitude aerial photographs of the study area at Demarcation Bay, Alaska. Abbreviation of vegetation type names are given in parentheses after each name.

30-ha Study plot			Study area		
	Percent coverage	Total coverage (ha)		Percent coverage	Total coverage (km^2)
Wet Meadows					
Water(W)	1.5	0.5	Water(W)	10.6	3.9
Wet Carex Meadow(CM)	6.3	1.9			
Dupontia Meadow(DM)	2.2	0.7	Meadow(M)	17.4	6.4
Arctophila Marsh(AM)	2.5	0.7			
Low Center Polygons(lcp)					
Dry Carex Meadow(DCM)	12.9	3.9			
Frost-boil Terrain(FB)	8.2	2.5	Low Relief lcp(LR)	16.5	6.1
Low Relief lcp(LR)	16.8	5.0			
Medium Relief lcp(MR)	7.7	2.3	Medium Relief lcp(MR)	35.9	13.3
High Relief lcp(HR)	1.0	0.3	High Relief lcp(HR)	1.6	0.6
Upland Habitats					
Tussock Slope(TS)	5.8	1.7	Tussock Slope(TS)	11.9	4.4
Terraced Slope(TER)*	9.3	2.8			
High Center Polygons(HCP)	16.7	5.0	High Center Polygons (HCP)	2.3	0.8
Coastal Habitats					
Gravel Beach(GB)**	-	-	Gravel Beach(GB)	0.7	0.3
Coastal Ponds(CP)	1.1	0.3	Coastal Ponds(CP)	0.4	0.1
Dry Coastal Polygons(DCP)**	-	-	Dry Coastal Polygons(DCP)	2.5	0.9
Slumping Banks(SB)**	-	-	Slumping Banks(SB)	0.2	0.1
Habitats Altered by Man***			Disturbed(DIST)		
Dozer Trail(DT)	5.5	1.7	-	-	-
Sled Tracks(ST)	2.4	0.7	-	-	-
		30.0			37.0

* May be mapped as tussock slope, low relief lcp or dry Carex meadow.
** Not present in study plot.
*** Not abundant enough for mapping from aerial photos.

types, the dozer trail and sled tracks, were not widespread enough to include in the larger scale analysis.

II. SMALL MAMMAL INVESTIGATION METHODS

In 1978, live trapping was conducted only on the 30-ha study plot. The plot was uniformly divided into 12 trap areas (160 m x 160 m). A 10 x 10 trap grid (100 traps) with trap intervals of 10 m was centered in each trap area. Although similarly diverse areas occurred at various locations, the dense interspersion of vegetation types in the 30-ha study plot was not typical of the study area, in which the most common vegetation types usually occupied large, homogeneous areas (Fig. 1). Few of the 100-trap grids in the study plot occupied a single, homogeneous vegetation type (Fig. 3). This was considered an advantage in determining habitat preferences of small mammals; although it was a disadvantage in calculating small mammal densities representative of each vegetation type in the study area. Each of the 12 trap areas was sampled for small mammals 3 times during the period 16 June to 18 August 1978, at approximately 1-month intervals. Traps were opened for a 48-h period during which they were checked at 8-h intervals. Before releasing, all captured animals were identified to species (names are as Hall 1981, except Dicrostonyx torquatus as per Jones et al. 1979), toe-clipped and ear-tagged for individual identification (except D. torquatus, lacking pinnae for attachment of tags), weighed and sexed, and apparent sexual condition and location

of capture were recorded. Sedge leaves were provided for nesting material and bait in 1978.

The 1978 trap results indicated that populations of the most common small mammal species had widely separated and localized distributions. The 1979 trap effort was modified, using habitat preference data, with the following aims: 1) to increase efficiency, 2) to verify habitat preference data from 1978, and 3) to sample larger, more homogeneous areas of preferred habitat for better information on densities.

In 1979, efforts were concentrated on the areas in which captures were most frequent in 1978: grids 4, 7, and 11, and a limited area of disturbed habitat, called the dozer trail, in grids 9, 10 and 11. Grids 4, 7 and 11 were sampled with 100 traps each, as in 1978. The dozer trail was sampled with a transect of 20 traps placed within 10 m of the trail wherever fresh sign was noted to the east of grid 11. The prediction of highest densities in these grids was tested by sampling throughout the 30-ha plot with 20 small quadrats of 4 traps each, placed at the corners of a 10 m x 10 m square, and located at random coordinates. Two additional 100-trap grids approximately 1.6 km south of the 30-ha plot were also sampled. These grids were placed in large areas of homogeneous vegetation/landform types similar to those types in which small mammals were captured on the 30-ha plot.

In addition to the 5 100-trap grids and 20 4-trap quadrats, another 17 quadrats of 4 traps each were set at locations within

1.6 km east and south of the 30-ha plot to sample all the major recognized habitats within the general area.

All trap areas were sampled simultaneously in 1979 at approximately 10-d intervals between 30 May and 1 September, thus yielding 10 trap periods. Captured animals were treated as in 1978, but use of ear tags was discontinued due to frequent loss and difficulty in attachment of tags. The trap period was 48 h, as in 1978, but traps were checked less frequently, at 8- to 12-h intervals depending on weather. Trap mortality was high during warm, sunny weather if animals were not promptly released. Nesting material of dry, raw cotton was provided and traps were baited with Purina Mouse Chow pellets.

Information on vegetation composition and cover was collected on 1 m x 1 m plots at all successful trap sites, at random locations in all trap grids, and at all trap sites in small quadrats both on and off the 30-ha plot. Methods used were as described in Section I (Vegetation Analysis Methods).

III. AVIAN INVESTIGATION METHODS

Common and scientific names used for bird species are those in AOU (1982). Bird nesting success and nest density were monitored only on the 30-ha study plot in both years. Nests were found by 3 methods: 1) observing and following individual birds on more or less systematic walks through the study plot, 2) dragging a 20 m x 1 cm white nylon rope systematically over the study plot to flush incubating birds, and

3) observing flushed birds during daily activities on the study site. The study area was searched daily for nests from 1 June to 1 July, the peak of nest initiation, and regularly but less often throughout the nesting season.

Nests were marked with flagged wooden stakes placed approximately 5 m from the nest, and situated so that an observer at the stake would find the nest in the direction of the camp antenna. In 1979 nest stakes were removed from Lapland longspur nests to eliminate their possible effects on fox predation, which was heavy in that year.

Nests were checked daily during laying and as anticipated hatch dates approached, but less frequently during early incubation. Nest contents were never disturbed or touched except during a banding effort in 1978 when incubating birds were captured on the nest. Capture and banding was relatively quick after some practice and had no apparent effect on nest success. In 1979, during incubation and rearing, longspur nests were given an especially wide berth when checked due to the aforementioned predation. During this period, nests were often recorded only as active or inactive based on presence of adults; females were not deliberately flushed and eggs and fledglings were not counted at every nest check.

IV. FOX BEHAVIOR INVESTIGATION METHODS

In 1978, the study was envisioned as monitoring prey populations within and outside of a fox-proof exclosure near an active fox den and

activities did not include observation of foxes. Only 1 of 4 known dens in the approximately 36 km^2 study area was active and 9 pups were raised there in 1978. Visits to the den were brief and infrequent to minimize disturbance. In retrospect, the many hours lost erecting what was envisioned as a fox-proof electric fence would have been more constructively used making behavioral observations at the den. The exclosure project was abandoned when deemed unfeasable in mid-season and efforts were thereafter devoted entirely to prey species investigations and vegetation analysis.

In 1979, I initiated an investigation of fox food habits, habitat use, and behavior through the use of radiotelemetry. Two types of traps were used to capture foxes: 1) number 2 Victor leg hold traps with offset and padded jaws, and 2) wire-mesh trap-door box traps. The trap effort began 12 May and continued until 13 June when 6 foxes were tagged. In addition to the trap effort during this period, 2 directional antennas were mounted on 9-m masts for use in locating foxes by triangulation.

Radio-tracking began 14 June. A triangulation schedule was devised to collect radio locations from the towers at 15-min intervals in 2 randomly-chosen hours each day. For behavioral observations, the season was divided into 10-d periods during which a minimum of 48 h of ground tracking was to be conducted in 8-h shifts. Shifts began at 0400 hours, 1200 hours and 2000 hours. Triangulations were taken approximately 1.5 h before each shift to locate the fox which was to be followed. A team of 2 observers then set out on foot with a

hand-held Yagi antenna, attempting to locate the fox and begin direct observations at the beginning of each shift. Behavioral observations were made from a distance of approximately 100 m or less, taking care to disturb the fox as little as possible and using the radio to relocate whenever the animal was lost from view. One member of each team acted as observer, using a tripod with binoculars or spotting scope and dictating behaviors and activities and habitat types traversed. The second member recorded these observations and time of occurrence with a stopwatch, pen and notebook. In addition to these 8-h shifts, observations were made whenever foxes were sighted from camp or while conducting daily activities in the study area.

Detailed maps of the fox's movements were made after each observation shift with emphasis on distance moved, habitats traversed, and amount of time spent in each habitat. Accuracy was assured by high quality aerial photographs of the study area. In addition, a detailed written description of locations during each observation period was prepared by the observer to aid in interpretation of the field notes.

For analysis, the data set was divided into 3 classes: 1) continuous tracking data for analysis of activity patterns and movements, 2) 60-s samples of observation bouts made during tracking and opportunistically whenever foxes were sighted for analysis of activity budget and habitat use, and 3) complete records of observations of foraging and social activities for analysis of behavior patterns and functions. Each ground-tracking shift provided

continuous data on activity patterns because the regularity of the radio-signal could be used to distinguish between active and resting foxes even if the animal was out of sight. Analysis of activity budgets required direct observation data. Although continuous records were made, observation records were sampled at 60-s intervals for activity budget analysis. Because direct observations are biased toward resting (a resting animal is easier to observe), activity budgets are presented in proportions of active hours, excluding all observations of resting foxes. Complete data records of foraging and social activities were used for analysis of food habits, for a functional analysis of scent marking, for an assessment of the ecological significance of caching, and for an analysis of the frequency of occurrence of social interactions.

VEGETATION ANALYSIS

I. RESULTS AND DISCUSSION

A total of 773 1-m^2 plots was sampled in 14 vegetation/landform types. Four types were sampled insufficiently for statistical descriptions: beach, dry coastal polygons, Arctophila marsh, and coastal ponds. However, none of these was widely distributed. A list of plant species encountered appears in Appendix 1.

Of the characteristics measured, 28 variables of percent cover, 12 variables of frequency of occurrence of species groups, and 3 physical variables were found useful in describing vegetation types. Cover values of 8 key species are considered individually because of their ubiquitousness or dominance in some types. Fifteen of the percent cover variables are composite values representing plant growth forms and/or phylogenetically related species groups. The remaining 5 percent cover variables are: moss, lichen, bare ground, water, and "other species," a composite group of species representing growth forms which rarely attained greater than 1% cover in any sample. The cover groups used are identified and their composition described in Appendix 2.

In all tundra vegetation types the abundance and ecological amplitude of the dominant species precludes the use of percent cover values alone in determining the type to which a plot belongs. Percent occurrence data for each species in each vegetation type provide

additional detail on actual species associations and are given in Appendix 3. The following groupings of species were used to examine frequency of occurrence of functional plant groups: 1) legumes, 2) Salix spp., 3) herbaceous species, 4) graminoid species, 5) heath associates, and 6) total woody species. Values for each of these variables in each vegetation/landform type are presented in Table 2. The species composition of each plant group is described in Appendix 2.

The variables used served to describe major vegetation/landform types, but did not in every case distinguish between sample plots in similar types because inadequate samples were available in some types, and because of small sample plot size. Webber (1978) measured percent cover and frequency of occurrence of plant species and several physical parameters on 1 m x 10 m plots at Barrow, Alaska. The larger plot size allowed use of cluster analysis to objectively identify plant communities (i.e. vegetation types) on the basis of species composition. Such an approach would have suited this investigation; however, the use of 1-m^2 plots prevented employing ordination techniques or cluster analysis in defining and defending major vegetation types required here. On the other hand, 1-m^2 plots were well-suited to identification of microhabitat use patterns of small mammals and nesting birds.

Table 2. Descriptions of vegetation types from randomly located 1-m^2 plots on the 30-ha study plot at Demarcation Bay, Alaska. Standard deviation for each parameter given in parentheses where appropriate. Codes are as defined in Table 1.

	Vegetation types													
	CM	DM	DCM	LR	MR	HR	TS	HCP	AM	TER	FB	DT	ST	CP
Number of samples	27	48	93	102	80	29	37	104	5	65	38	79	57	7
Physical parameters														
Average microrelief (cm)	18.4 (17.9)	29.4 (13.0)	28.1 (8.3)	30.5 (12.8)	35.5 (20.7)	74.6 (41.0)	33.7 (8.5)	41.0 (21.5)	10.2 (14.4)	37.0 (12.6)	34.7 (6.9)	47.9 (32.8)	35.3 (11.9)	21.3 (9.9)
Average number of species	6.1 (3.6)	8.8 (2.5)	8.4 (2.6)	8.1 (3.3)	9.7 (3.8)	11.1 (2.9)	14.4 (3.6)	13.4 (3.4)	3.4 (1.8)	10.5 (3.4)	12.9 (3.9)	2.0 (4.0)	10.6 (3.4)	7.1 (4.3)
Average height of vegetation (cm)	67.9 (75.3)	29.7 (13.5)	21.2 (7.8)	22.2 (8.3)	23.8 (11.6)	15.7 (6.4)	12.4 (5.8)	15.1 (6.5)	101.6 (71.8)	22.3 (10.0)	19.2 (8.4)	24.6 (15.9)	23.6 (7.4)	9.6 (3.8)
Average moisture index	4.3 (1.5)	3.3 (0.8)	3.0 (1.4)	2.7 (1.4)	3.0 (1.4)	1.8 (0.9)	1.3 (0.4)	1.5 (0.8)	5.6 (0.5)	2.3 (1.3)	1.9 (1.0)	3.1 (1.6)	2.8 (1.3)	4.1 (1.5)
Percent cover values														
Carex aquatilis	65.4 (25.2)	7.3 (14.0)	67.5 (23.5)	62.9 (29.0)	49.4 (30.3)	33.4 (28.1)	13.9 (27.3)	14.9 (26.9)	30.0 (34.8)	50.7 (29.5)	38.9 (33.5)	43.4 (33.2)	63.6 (39.5)	2.1 (5.7)
Carex bigelowii	-	0.2 (1.4)	0.7 (7.2)	3.1 (14.2)	0.7 (6.7)	0.9 (4.6)	28.5 (26.0)	22.0 (28.2)	-	4.4 (13.1)	14.4 (24.6)	1.3 (8.8)	5.0 (14.7)	-
Other rhizomatous Cyperaceae	1.5 (7.7)	1.3 (5.3)	0.7 (4.8)	2.1 (10.9)	3.2 (12.5)	-	-	0.6 (4.6)	-	6.8 (18.6)	2.2 (6.9)	0.6 (2.8)	3.0 (11.7)	-
Eriophorum angustifolium	-	1.7 (4.0)	1.7 (7.8)	0.1 (1.1)	2.2 (8.0)	-	-	0.3 (2.1)	-	0.5 (3.7)	2.8 (9.8)	7.0 (14.4)	2.6 (10.1)	-
Dupontia fischeri	4.4 (13.3)	77.0 (24.0)	1.0 (5.5)	3.9 (14.4)	12.8 (25.7)	0.2 (0.9)	-	2.4 (11.9)	-	3.3 (12.0)	1.1 (5.1)	2.3 (9.1)	0.3 (2.0)	-
Other rhizomatous Graminae	0.1 (0.3)	2.5 (9.2)	1.5 (6.8)	1.3 (8.0)	0.7 (4.6)	-	-	0.4 (2.8)	24.0 (14.7)	0.7 (3.5)	-	1.2 (4.8)	1.3 (4.3)	-
Moss	8.4 (13.2)	0.2 (1.4)	6.6 (9.8)	6.5 (10.4)	6.6 (10.2)	16.4 (17.1)	8.4 (8.0)	9.3 (11.8)	2.0 (2.7)	7.2 (11.7)	6.4 (8.4)	10.2 (15.3)	3.4 (7.1)	1.4 (3.8)
Lichen	-	-	0.5 (2.6)	0.5 (2.1)	1.4 (5.0)	13.3 (13.8)	9.0 (13.9)	5.0 (9.8)	-	1.1 (3.3)	5.7 (8.3)	1.4 (6.6)	0.8 (3.2)	0.7 (1.9)
Salix reticulata	0.7 (2.3)	0.0 (0.3)	5.4 (9.6)	5.6 (8.5)	3.8 (6.6)	2.5 (4.8)	9.1 (8.8)	7.3 (8.5)	-	6.6 (7.9)	6.3 (7.7)	1.2 (3.7)	3.2 (6.0)	2.1 (5.7)
Salix arctica	5.9 (15.1)	1.1 (7.2)	8.7 (10.5)	5.3 (8.0)	6.8 (11.5)	4.6 (7.7)	5.8 (8.2)	12.4 (11.9)	-	5.0 (8.6)	8.0 (9.2)	3.8 (8.5)	6.8 (10.4)	0.7 (1.9)
Salix phlebophylla	-	-	0.0 (0.3)	-	0.7 (5.1)	10.1 (13.3)	1.8 (8.3)	5.5 (10.1)	-	0.2 (1.2)	0.9 (3.6)	0.2 (1.0)	0.3 (2.5)	-
Poa spp.	-	1.0 (4.6)	0.3 (3.1)	0.1 (1.3)	2.2 (6.2)	2.5 (7.1)	0.5 (1.5)	1.8 (7.1)	-	0.7 (3.4)	1.2 (6.5)	4.1 (13.3)	0.6 (3.4)	-

Table 2. (cont.)

	Vegetation types													
	CM	DM	DCM	LR	MR	HR	TS	HCP	AM	TER	FB	DT	ST	CP
Eriophorum vaginatum	-	-	-	0.2	0.1	0.3	13.0	9.2	-	0.2	1.4	-	2.9	-
				(1.1)	(0.6)	(1.9)	(16.0)	(13.9)		(1.9)	(6.6)		(9.1)	
Bare ground	2.4	0.6	0.5	3.3	3.7	2.8	0.1	0.6	4.0	3.8	1.4	13.4	2.5	14.3
	(8.1)	(2.4)	(3.4)	(14.5)	(9.7)	(5.4)	(0.5)	(3.4)	(6.5)	(15.9)	(4.2)	(23.3)	(5.1)	(37.8)
Water	10.3	1.6	-	0.1	0.9	-	-	-	40.0	-	0.1	0.4	0.3	14.3
	(21.6)	(10.8)		(1.0)	(4.2)				(34.5)		(0.8)	(3.4)	(1.7)	(37.8)
Tufted Cyperaceae	-	-	2.0	0.8	1.3	2.6	-	0.5	-	3.3	-	1.7	3.2	-
			(10.4)	(5.6)	(11.2)	(7.1)		(4.0)		(12.5)		(11.3)	(13.5)	
Tufted Graminae	-	0.3	-	0.1	0.1	0.4	0.3	1.7	-	-	1.4	0.5	0.6	-
		(2.2)		(1.2)	(0.6)	(1.4)	(1.4)	(6.5)			(6.6)	(2.5)	(3.5)	
Heath	0.2	-	1.9	3.8	1.8	6.6	7.0	3.6	-	4.5	7.4	0.2	1.5	-
	(1.0)		(5.2)	(8.8)	(7.1)	(10.6)	(11.9)	(10.7)		(8.1)	(10.7)	(2.2)	(6.2)	
Luzula spp.	-	-	-	-	0.0	-	0.1	0.7	-	0.1	-	1.6	-	-
					(0.2)		(0.8)	(2.3)		(0.6)		(5.0)		
Saxifragaceae	0.6	3.7	0.1	0.0	0.2	-	-	0.0	-	0.1	0.0	1.1	0.1	1.7
	(2.9)	(5.9)	(0.7)	(0.5)	(1.1)			(0.1)		(0.6)	(0.3)	(3.7)	(0.5)	(3.7)
Caryophyllaceae	-	0.3	-	-	0.1	0.9	-	0.1	-	-	0.1	2.4	-	-
		(1.6)			(0.6)	(4.6)		(1.1)			(0.8)	(7.0)		
Other	-	1.0	0.6	0.1	0.5	1.4	1.6	0.2	-	0.8	0.3	1.0	-	64.0
		(4.8)	(2.3)	(1.1)	(3.1)	(7.4)	(4.4)	(1.5)		(5.0)	(1.1)	(2.7)		(45.4)
Total rhizomatous Cyperaceae	64.5	10.5	70.6	69.0	55.7	33.2	42.4	37.7	30.0	62.4	58.3	52.3	74.2	2.1
	(27.5)	(14.1)	(21.4)	(23.2)	(29.8)	(28.2)	(26.3)	(28.8)	(34.8)	(23.9)	(26.1)	(36.3)	(31.6)	(5.7)
Total Graminae	4.4	81.8	2.8	4.9	15.8	5.3	0.8	6.4	24.0	4.7	3.7	8.2	2.8	62.6
	(13.1)	(21.0)	(10.1)	(15.5)	(26.6)	(14.1)	(2.8)	(15.5)	(14.7)	(13.9)	(10.2)	(16.3)	(8.3)	(44.2)
Total Salix	6.4	1.1	14.7	10.8	11.3	17.4	17.0	25.2	-	11.8	15.3	5.1	10.4	2.9
	(14.8)	(7.2)	(15.9)	(11.1)	(15.2)	(14.3)	(13.1)	(14.3)		(11.9)	(12.6)	(9.6)	(13.3)	(7.6)
Total herbaceous	0.7	4.1	2.0	4.0	2.1	7.4	8.4	4.0	-	5.4	7.8	4.8	1.6	1.7
	(2.9)	(6.8)	(5.2)	(8.9)	(7.1)	(10.9)	(13.1)	(10.9)		(9.1)	(11.5)	(11.3)	(6.2)	(3.7)
Total graminoid	68.9	92.4	75.4	74.8	72.8	41.3	56.3	54.6	48.0	70.7	63.5	63.9	83.1	64.7
	(27.3)	(13.7)	(18.2)	(18.9)	(21.7)	(25.0)	(23.2)	(24.0)	(31.9)	(18.9)	(24.6)	(33.9)	(23.0)	(45.8)
Total woody	6.4	1.1	14.2	11.1	12.9	22.3	16.8	25.3	-	11.9	15.3	5.1	10.4	2.9
	(14.8)	(7.2)	(15.5)	(11.2)	(15.8)	(15.5)	(13.2)	(14.3)		(11.9)	(12.6)	(9.6)	(13.3)	(7.6)
Average number of species in group														
Legumes	-	-	-	-	-	-	0.1	0.1	-	-	0.2	-	0.0	-
							(0.3)	(0.3)			(0.7)		(0.1)	
Salix	0.7	0.3	1.6	1.6	1.4	2.2	2.2	2.4	0.4	1.7	2.0	1.0	1.6	0.3
	(0.9)	(0.5)	(0.7)	(0.7)	(0.8)	(0.7)	(0.5)	(0.6)	(0.9)	(0.8)	(0.6)	(0.8)	(0.7)	(0.8)

Table 2. (cont.)

	Vegetation types													
	CM	DM	DCM	LR	MR	HR	TS	HCP	AM	TER	FB	DT	ST	CP
Herbaceous	2.4	5.1	2.9	2.7	3.8	3.0	6.2	5.3	1.0	4.1	5.7	4.8	4.7	3.1
	(2.4)	(1.5)	(1.9)	(1.8)	(2.2)	(1.4)	(2.6)	(2.3)	(1.0)	(2.2)	(2.6)	(2.2)	(1.9)	(2.8)
Graminoid	1.7	2.7	1.7	1.7	2.4	2.9	2.8	2.8	1.6	2.0	2.4	3.3	2.6	2.4
	(1.2)	(1.2)	(0.9)	(1.0)	(1.4)	(2.1)	(1.3)	(1.3)	(0.9)	(1.1)	(1.2)	(1.7)	(1.5)	(0.8)
Heath	0.2	0.0	0.6	0.6	0.4	1.3	1.0	0.8	-	1.1	1.0	0.1	0.5	0.3
	(0.4)	(0.1)	(0.7)	(0.5)	(0.7)	(1.0)	(0.5)	(0.7)		(0.9)	(0.5)	(0.3)	(0.6)	(0.8)
Woody	0.7	0.3	1.7	1.6	1.7	3.1	2.3	2.7	0.4	1.9	2.0	1.0	1.6	0.4
	(0.9)	(0.5)	(0.9)	(0.8)	(1.1)	(1.2)	(0.6)	(0.8)	(0.9)	(0.9)	(0.6)	(0.8)	(0.8)	(1.1)
Percent of plots with group present														
Legumes	-	-	-	-	-	-	10.8	7.7	-	-	10.5	-	1.8	-
Salix	48.1	31.3	95.7	88.2	83.8	100.0	100.0	100.0	20.0	89.2	97.4	74.7	93.0	14.3
Herbaceous	70.4	97.9	90.3	89.2	92.5	96.6	100.0	99.0	60.0	90.8	100.0	97.5	98.2	85.7
Graminoid	100.0	100.0	100.0	98.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	98.7	100.0	100.0
Heath	22.2	2.1	52.7	54.9	32.5	82.8	89.2	65.4	-	70.8	89.5	7.6	40.4	14.3
Woody	48.1	31.3	95.7	88.2	83.8	100.0	100.0	100.0	20.0	89.2	97.4	74.7	93.0	14.3
Total number of species	29	40	45	47	55	52	49	55	10	48	44	45	48	23

II. VEGETATION TYPE DESCRIPTIONS

Distributions of 17 recognized vegetation/landform types in the study area and on the 30-ha study plot are presented in Table 1. The summary which follows is drawn from data presented in Table 2 and Appendix 3. Several of the types identified and sampled on the 30-ha study plot were limited in areal extent or could not be mapped from the aerial photos. Those vegetation types are considered microhabitats of larger vegetation types in the study area map. These modifications are noted in the descriptions where appropriate.

A. Wet meadows

Meadows are areas of predominantly graminoid vegetation with little or no microrelief. Two types of wet meadow were recognized in analysis of vegetation patterns and distribution of prey species on the 30-ha plot: wet Carex meadow and Dupontia meadow. Dupontia meadow and Arctophila marsh were combined with wet Carex meadow in study area maps because of their limited areal extents and similar physiognomies (Table 1). Wet meadow was a widespread vegetation type, the second largest in total areal extent in the study area (Table 1). It occupied extensive homogeneous areas dominated by Carex aquatilis, often accompanied by sub-dominants ranging from Eriophorum angustifolium to Dupontia fischeri to Arctophila fulva, each of which became dominant to the exclusion of Carex in extremes of soil moisture or nutrient content (Webber 1978). Wet meadows also occurred in

small, discrete sites, such as drainage areas, pond margins, and numerous small marshes.

Wet Carex meadow

Wet Carex meadows were typically large homogeneous areas, where robust stands of C. aquatilis (averaging 68 cm in height) dominated. Although distinct polygonization was often present, microrelief was relatively low and had little effect on vegetation height or moisture. Total graminoid cover averaged 68.9%, and consisted almost entirely of C. aquatilis. This is the only vegetation type in which C. aquatilis flowered profusely and formed a thick canopy. The plant community had low diversity, 6.1 species per m^2 (SD=3.60), which is typical of wet tundra. Next to C. aquatilis, moss (8.4%) and water (10.3%) had the highest average cover values. Twenty-nine plant species occurred in Carex meadows, but C. aquatilis was the only species which occurred in more than 50% of the samples (Appendix 3). Most herbaceous species were confined to the understory of raised polygon ridges and herbs occurred in only 70.4% of plots sampled, having an average cover value of only 0.7%.

Dupontia meadow

Dupontia meadows were not widespread and, in the Demarcation Bay area, occupied small drainage areas near the coast. Although limited in areal extent, Dupontia meadow was a distinct vegetation type and provided habitat for Microtus oeconomus; nearly all captures of M. oeconomus were in a Dupontia meadow. Dupontia meadow was physiognomically similar to Carex meadow, but D. fischeri was dominant

(77.0% cover). C. aquatilis was co-dominant in some stands but occurred in only 31.3% of samples and attained an average cover value of only 7.3%. (Only one other vegetation type, coastal ponds, had a lower value of cover for C. aquatilis.) Dupontia meadow had the highest average cover of graminoid forms of any vegetation type sampled (Table 2). The average diversity of graminoid forms was also high, 2.7 species per m^2, due to the high presence of E. angustifolium (found in 58% of plots sampled), Poa arctica (27%), and Eriophorum scheuchzeri (4.4%), in addition to C. aquatilis. Other vegetation types dominated by graminoids typically had fewer graminoid species. Although microrelief in meadows had little effect on dominance or vegetation height, it did affect the species composition of the herbaceous understory in Dupontia meadows. The average number of species per m^2 (8.81) was higher than in Carex meadow. Forty plant species occurred in Dupontia meadow, and 6 occurred in more than half of the plots sampled: Saxifraga cernua, D. fischeri, Chrysosplenium tetrandum, Melandrium apetalum, E. angustifolium, and Cochlearea officinalis. In addition to E. angustifolium and E. scheuchzeri, the herbs, Chrysosplenium tetrandum, Cochlearia officinalis, M. apetalum, S. cernua and Stellaria crassifolia occurred with greatest frequency in Dupontia meadow. This was the only wet vegetation type in which herbaceous species achieved high frequency and diversity; the average number of herbaceous species per m^2 was 5.1 and their frequency of occurrence was 97.9%. Average cover of herbs (4%) was in the midrange of values for those vegetation types

sampled (Table 2). The family Saxifragaceae was the most important herbaceous group, and occurred in 97.9% of plots sampled, with 2.0 species per m^2, and an average cover value of 3.7%. Woody species had their lowest cover value (1.1%) in Dupontia meadow, and were much less important in this type than they were in Carex meadow.

Arctophila marsh

Arctophila fulva grew almost exclusively in areas retaining standing water throughout summer and in such areas was dominant cover to the exclusion of nearly all other species. Graminoids (A. fulva, D. fischeri, C. aquatilis, and E. angustifolium) grew to their greatest height in this type, averaging 102 cm (SD=72), though they had the lowest average percent cover of any type sampled (48%) due to low culm density. Ten species occurred in sample plots in Arctophila marsh (n=5), but only 6 are typical of deeper water areas: A. fulva, Ranunculus pallasii, Ranunculus gmelini, Caltha palustris, C. aquatilis, and E. angustifolium. The other species occurred in samples on marsh edges. Arctophila marshes were common in the Demarcation Bay area, sometimes covering large areas but frequently limited to the edges of shallow lakes and ponds. Arctophila marsh was typically bordered by wet Carex meadow and small areas of open water capable of supporting nesting red-throated (Gavia stellata) or arctic loons (G. arctica). Marshes are particularly important areas for feeding and flocking of post-breeding birds when the vegetation is most luxuriant in July and August.

B. Low center polygons

Low center polygons (lcp) are the most widespread physiognomic feature of arctic tundra and are highly variable in microrelief and associated drainage and vegetation patterns. Three general vegetation/landform types were distinguished here based on the relief gradient: low relief lcp, medium relief lcp, and high relief lcp. Frost-boil terrain and dry meadow also appeared as polygonized tundra in aerial photos and were combined with low relief lcp on study area maps. All these vegetation types occurred along a gradient, making drawn boundaries between types somewhat subjective in some cases. Because moisture changes, resulting from microrelief variation, determine species composition, the species composition and cover of wet, dry and mesic microhabitats are quite similar to the composition and cover of those microhabitats occurring in other vegetation types.

Dry Carex meadow

Dry Carex meadow was low relief, indistinctly polygonized terrain (viewed from the ground), usually extensive in area and often occupying large basins surrounded by higher ground. Polygons in dry Carex meadow retained moisture for brief periods in troughs and centers and though the vegetation type was flooded during break-ups it became relatively dry between rainstorms in mid-summer. Perhaps as a result of the temporal variability in moisture, vegetation was poorly developed with graminoid species of low average height (21 cm) having few flowering culms. C. aquatilis dominated, with an average cover of 67.5%, but lack of fruiting bodies made identification of graminoids

difficult. Other graminoids, especially Carex species, were present in significant amounts. The species list includes 6 species of Carex, 2 of Eriophorum and 6 other graminoid species, but the average number of graminoid species identified per plot is low (1.7), due in part to the lack of flowering culms. Low ridges often supported a distinct flora dominated by prostrate willows. All 4 species of Salix occurred in dry Carex meadow and all were more frequent there than they were in wet meadows. Woody species composition was dominated by Salix arctica (8.7% cover) and Salix reticulata (5.4%). Woody species occurred in 95% of sample plots.

Forty-five species occurred in dry meadow, and 4 occurred in more than half of the plots sampled: C. aquatilis, S. arctica, Pedicularis kaneii, and Polygonum viviparum. In general, the species list includes members favoring drier conditions than existed in wet Carex meadow, though none are restricted to this vegetation type. Salix lanata and P. kaneii occurred more frequently in dry Carex meadow than in any other vegetation type.

Frost-boil terrain

This vegetation/landform type occurred in small patches distributed throughout drier areas of low relief polygons and dry meadows. It is a distinct vegetation association, as shown by species occurrence and percent cover values, but could not be mapped from aerial photos. Frost-boil areas were vegetatively diverse (12.9 species per m^2), and dry. Polygonization was of low relief and indistinct, most relief being provided by frost-boils. One-fourth to

one-third of the boils were very sparsely vegetated or barren, with 1.4% of the total ground surface in the type barren. Legumes appeared to be important components of frost-boil vegetation. Although none occurred with a frequency greater than 8%, all 4 of the legumes recorded in sampled plots were present in this type. The average number of legume species per plot was also highest in frost-boil areas at 0.2. Legumes were present on 10.5% of the plots sampled. Graminoid forms dominated in interboil areas; Carex aquatilis (38.9% cover) and Carex bigelowii (14.4% cover) were dominant. Average cover of woody species was similar to that in dry Carex meadow (15.3%). Heath cover (7.4%) and total herbaceous cover (7.8%) were much higher than in surrounding low relief lcp. Herbaceous species were quite diverse in frost-boil terrain (5.7 species per m^2) and herbs occurred in 100% of the plots sampled. Heath species had the highest frequency of occurrence in frost-boil areas, appearing in 89.5% of the samples. Astragalus alpinus, Astragalus umbellatus, Equisetum spp., Oxytropis nigrescens, Pedicularis sudetica, Polemonium acutiflorum, and Senecio atropurpureus occurred more frequently here than in any other vegetation type. In all, 44 species occurred in frost-boil areas.

Low relief lcp

Low relief lcp was physiognomically different from dry Carex meadow in that polygons were composed of distinct troughs, ridges, and centers with mostly complete borders and microrelief was slightly greater. Low relief lcp also differed from dry Carex meadow in the

distribution of plant species within microhabitats; with microrelief, ridges, troughs, and centers acquired their own plant associations. This was reflected in the slightly lower and more variable number of species per plot, 8.1 (SD=3.30). As in dry meadow, C. aquatilis dominated (62.9% cover), but D. fischeri was more abundant in wetter troughs and C. bigelowii on drier ridges. Salix and heath cover were less than in dry meadow as woody and heath vegetation were restricted to ridges. Forty-seven plant species occurred in low relief lcp. These include species representing a wider range of moisture preferences, both more mesic and more xeric than was true for dry meadows.

Medium relief lcp

In general, the boundaries between microhabitats of ridge, trough, and center were more abrupt and their plant associations more distinct in medium relief lcp than in low relief lcp. Ridges were wider and higher than in low relief lcp with a subsequent increase in cover values of woody species from 11.1 to 12.9%. Woody vegetation cover was restricted almost entirely to ridges. C. aquatilis dominated, especially in polygon centers, and attained an average cover of 49.4%. D. fischeri was important in wet troughs and had an average cover of 12.8%. The average number of species per m^2 increased along the gradient from low to medium to high relief lcp (8.1, 9.7, and 11.1, respectively), due primarily to increased diversity of xerophiles. Fifty-five plant species occurred in samples. Due to the increased individuality of microhabitat

communities sampled with the 1-m^2 plots, only 4 species occurred in more than half of the plots: C. aquatilis, S. arctica, P. viviparum, and S. cernua.

High relief lcp

High relief lcp was quite limited in areal extent, occupying only 2.3% (0.8 km^2) of the Demarcation Bay tundra. However, this is probably an underestimate due to the frequent occurrence of high relief in units too small to map. Polygons in high relief lcp were typically smaller in diameter than those in lower relief lcp and supported a distinct xeric community on their ridges. Troughs and centers varied greatly in moisture; some were permanently ponded and others were well-drained, becoming dry in mid-summer. Microrelief was greater here than in any other vegetation type, averaging 75 cm. The average number of plant species per m^2 was greater and average vegetation height lower than in lower relief polygons as graminoids were less dominant on the wide ridges. Average cover of graminoids was lower than in any other vegetation type (41.3%). The species list includes 52 species. C. aquatilis remained dominant, but average cover of C. aquatilis was only 33.4%. Poa spp. attained a cover value of 2.5, making it the only other graminoid with an average cover of greater than 1%. However, the graminoids, Carex saxatilis, Hierochloe alpina, Luzula arctica, Alopecurus alpinus and Trisetum spicatum, all attained their highest frequency of occurrence in high relief lcp and can be considered characteristic of xeric ridges in that type. Heath species were also characteristic; they were present in 82.8% of the

samples with 6.6% cover, and 1.3 species per m^2. The heath associates, Empetrum nigrum, Vaccinium vitis-idaea and Ledum palustre occurred most frequently in high relief lcp. Salix phlebophylla reached by far its greatest average cover and Salix reticulata and S. arctica were also common. Woody species attained a cover value second only to that for high center polygons, and occurred in 100% of the plots sampled. The average number of woody species per m^2 was 3.1, greater than for any other vegetation type. Moss and lichen cover values peaked in high relief lcp at 16.4 and 13.3%, respectively. Herbaceous species also achieved a relatively high cover value. Artemisia arctica, Eutrema edwardsii, Oxyria digyna, Petasites frigidus, Potentilla spp., Saxifraga oppositifolia, Silene acaulis, and Valeriana capitata occurred more frequently here than in any other vegetation type. Six species occurred in more than half of the samples: C. aquatilis, S. arctica, S. reticulata, P. viviparum, V. vitis-idaea, and P. sudetica.

C. Upland vegetation types

Tussock slope

Tussock slope occurred on all gently sloping hillsides and was dominant in the foothills directly south of the study area. All sampling was conducted in proximity to the coast (approx. 200 to 500 m) where density and vigor of tussocks were reduced; therefore, differences in community composition between the study plot and inland sites are expected. Tussock slope was a uniformly dry plant

association (average moisture index 1.3, SD=0.44) of high diversity. The average number of species per m^2 (14.4) was greater than in any other vegetation type. The vegetation was low-growing, at least in coastal locations, with average vegetation height of 12 cm. In the most coastal locations sampled, Eriophorum vaginatum tussocks were small and sparse, and many tussock heads appeared dead or dying. Due to its lack of vitality, E. vaginatum attained a ground cover of only 13.0% in sampled plots. C. bigelowii (28.5% cover) and C. aquatilis (13.9% cover) were the dominant species. Tussock slopes typically were indistinctly polygonized; E. vaginatum occupied raised centers and C. bigelowii/C. aquatilis were co-dominant in broad well-drained troughs. Herbaceous species occurred in 100% of the samples. Total herbaceous cover was greatest in tussock slope (8.4%) and diversity of herbs highest (6.2 species per m^2). The herbs, Lagotis glauca, Parrya nudicaulis and Pyrola grandiflora, were common nowhere else, and the following herbs occurred most frequently in tussock slope: Polygonum bistorta, Saussurea angustifolia, Minuarta arctica, Cardamine pratensis, Oxytropis maydelliana, and Papaver hultenii. In all, 49 plant species occurred in tussock slope, 8 in more than half of the plots sampled: S. reticulata, Dryas integrifolia, S. arctica, Stellaria longipes, P. viviparum, C. bigelowii, Pedicularis langsdorffii, and E. vaginatum. Woody plants occurred in every plot sampled and total woody cover was high. All 4 species of Salix occurred in tussock slope and averaged 2.2 Salix species per plot. Heath species were also common (89.2% occurrence) and attained 7.0%

cover. Legumes had their highest frequency of occurrence in tussock slope (10.8% occurrence). Differences noted in more inland locations include increased importance and diversity of herbaceous and heath species between tussocks and more dense and vigorous tussock growth masking polygonization with overall dominance of E. vaginatum.

Terraced slope

This vegetation/landform type was quite restricted in areal extent and could not be mapped from aerial photos. Terraced slope occurred on gentle slopes adjacent to tussock slope vegetation, low relief lcp, or dry Carex meadow, and it was mapped as any of those types. In vegetation distribution patterns and cover, terraced slope was most similar to dry Carex meadow, differing mainly in physiognomy, i.e. occurring in areas of gentle slope with impeded drainage. Polygonization was confused by solifluction ridges, which were more important than polygonal microrelief in determining species distributions. Solifluction ridges throughout the type formed hummocks which generally followed contour lines. These created a terraced effect with small ephemeral ponds on various levels, some of which were entirely devoid of vascular vegetation. Species frequencies and cover values differed little from those found in dry meadow. The vegetation was generally poorly developed, dominated by low C. aquatilis (50.7% cover) with few flowering culms. C. bigelowii (4.4%), D. fischeri (3.3%), heath (4.5%) and herbaceous species (5.4%) all had greater cover values in terraced slope than in dry meadow. The average number of herbaceous species per m^2 (4.1) was much

greater than in dry meadow. Cassiope tetragona occurred most frequently here and in dry meadow and Rubus chamaemorus occurred far more frequently here than in any other vegetation type (26.2% occurrence). These species are often indicative of areas which collect snow during winter, which the southwest slope of the sampled area would facilitate. As in dry meadow, moisture was highly variable temporally; many small ponds formed in spring and after heavy rains but the terrain became quite xeric during prolonged dry periods.

High center polygons

High center polygons occurred on broad summit areas of low hills and were characterized by intimate juxtaposition of wet and dry plant associations and numerous deep ponds in expanded troughs. Drainage was poorer than in tussock slopes and the increased moisture favored C. aquatilis (14.9% cover) and D. fischeri (2.4% cover) which dominated in wet troughs. Species diversity was high: 13.4 species per m^2, with a relatively even distribution of percent cover values among major cover groups. In polygon centers, C. bigelowii and E. vaginatum were co-dominant, with cover values of 22.0 and 9.2%, respectively. Borders between troughs and centers were not abrupt, providing ample mesic areas for growth of S. arctica (12.4% cover) in association with C. aquatilis. The average cover value of woody vegetation was highest in high center polygons at 25.3%, and consisted almost entirely of Salix spp. Average number of Salix spp. per m^2 was greatest in high center polygons (2.4), and S. phlebophylla attained its highest frequency here (53%). Fifty-five plant species

were found in high center polygons, and 20 species occurred in more than 20% of the sampled plots. The species frequencies in high center polygons were quite similar to those in tussock slope, excepting a decrease in frequency of D. integrifolia, L. glauca and P. bistorta and an increase in V. vitis-idaea. Eritrichium aretioides and Polemonium boreale occurred only in high center polygons and dry coastal polygons. Luzula confusa, Cardamine hyperborea, Pedicularis capitata and S. longipes occurred more frequently in high center polygons than in any other vegetation type. Legumes were present in 7.7% of the samples.

D. Coastal vegetation types

Gravel beach

Beaches were limited to 0.7% of the study area, covering only 0.2 km^2. The upper reaches of sandy beaches supported sparse growth of a few specialists including: Mertensia maritima, Honkenya peploides and Puccinelia phryganodes. Beaches grade into turf of dwarf forms of Carex spp. and D. fischeri with Potentilla spp., Cerastium beeringianum, S. crassifolia, and D. integrifolia.

Coastal ponds

Brackish coastal ponds or pond systems occurred at intervals along the coast where wide drainage areas in low polygonized tundra met the raised gravel beach. Some coastal pond systems formed well-developed "salt marshes", but more frequently they were limited in extent and poorly developed due to the rapidly eroding coastline.

As a type, the ponds and adjacent strands and flooded polygon troughs covered only 0.4% of the study area, approximately 0.1 km^2. The water level of these ponds varied between years and within a season as shifting sand or wave action periodically drained or impounded them. Large waves also periodically broke over the beach and flooded such areas with salt water. The only common aquatic and emergent plants were Hippuris tetraphylla and R. gmelini. The brackish water was often dark brown to black in color. In some areas pond shores were quite complex, following deep polygon troughs and isolating many polygon centers and ridges as small islands. Much of the terrain on pond shores was unvegetated, particularly during low water.

The vegetation in coastal ponds was quite low (10 cm ave), resulting in part from the preponderance of bare ground and water (28.6% cover). Also, the dominant graminoid forms were low, turf-forming species: P. phryganodes, Carex ursina, and Carex subspathacea. Graminoid species covered 64.7% of the area, and included dwarfed D. fischeri and C. aquatilis in the plots furthest from the coast. The herbaceous cover value of 1.7% was composed entirely of members of the family Saxifragaceae; some Cruciferae and Caryophyllaceae also occurred but not in sample plots.

Dry coastal polygons

These well-drained, flat-topped polygons near the coast supported a distinct vegetation association, including some plant species found nowhere else in the study area. In general, the vegetation was poorly developed with much bare peat exposed through wind action on coastal

bluffs. The flora included the following specialized species: Sedum rosea, Primula borealis, H. alpina, Luzula wahlenbergii, E. aretioides, S. oppositifolia, Juncus castaneus, M. arctica, O. nigrescens, P. nudicaulis, Potentilla spp., S. acaulis, S. crassifolia and T. spicatum.

Slumping banks

Slumping banks were unique but unimportant unvegetated areas covering 0.2% (0.05 km^2) of the study area. These areas were limited to coastal bluffs and lake shores where wave action exposed permafrost and melting caused a bank of jumbled peat and turf. Aside from the upper surfaces of large blocks of slumping upland tundra, vegetation was limited to O. digyna and Senecio congestus, which colonized the disturbed peat.

E. Disturbed vegetation types

Disturbed vegetation types included gravel pads, and tracks and trails of vehicles. They were generally limited in areal extent, but were well-represented on the 30-ha study plot. Sled and wheeled-vehicle tracks represented the least drastic alteration of vegetation patterns, while the tracks of a bulldozer across the study plot may have altered the vegetation over a much larger area than the trail itself because of changed drainage patterns.

Dozer trail

The dozer trail was a drainage ditch with dry mounds of peat on either side. The extent of drying of surrounding tundra was

impossible to determine although the trough was a small stream during break-up and after large rainstorms. Although the trail extended approximately 1.4 km through medium relief lcp, a wet meadow drainage area and along a marsh edge (Fig. 3), the trough and mounds retained a high degree of consistency throughout. The trough was about 4 m wide and varied from wet to flooded, supporting a rich growth of C. aquatilis mixed with E. angustifolium and D. fischeri. Some true aquatics and emergents (A. fulva and Ranunculus spp.) appeared in the deepest areas. The adjacent mounds of peat supported a more unique assemblage of predominantly herbaceous vegetation. Forty-five species, of which 18 were herbaceous, occurred on the dozer trail. The amounts of bare ground and moss were high (13.4 and 10.2%), while cover of graminoid species (63.9%) was relatively low. Although woody species were present, their cover values were not high (5.1%), perhaps because of limited time since colonization and slow growth of these forms. C. beeringianum, Draba spp., Eriophorum russeolum, Juncus arcticus, Juncus biglumis, J. castaneus, Luzula multiflora, P. arctica, and Saxifraga foliosa occurred more frequently in the dozer trail than in other vegetation types. Percent cover of Caryophyllaceae was highest in the dozer trail, as were percent cover of Poa and Luzula species.

Sled tracks

Sled tracks had a less drastic effect on plant associations than the dozer trail and no noticeable effect on immediately adjacent tundra. Although they may not deserve treatment as a separate type,

sample plots within sled tracks were separated from analysis of surrounding vegetation to avoid their unknown effect on other vegetation type descriptions. A 20 to 30 m wide area contained approximately 50 tracks, each 20 to 30 cm wide, and extended from NW to SE through the study area from the DEW line site (Fig. 3). The tracks ranged from 10 to 30 cm deep and crossed high center polygon, tussock slope, low relief lcp and dry Carex meadow in the study plot. They did not greatly alter drainage and the general character of the original community was retained, although the scars superimposed their own microrelief patterns on existing physiognomy. It appeared that the disturbance resulted in increased frequency of occurrence of some herbaceous forms, including legumes and mustards, but the effects were minor.

SMALL MAMMAL INVESTIGATION

I. RESULTS

Four species of small mammals were captured in the study area: Microtus oeconomus, Lemmus sibericus, Dicrostonyx torquatus and Sorex cinereus. Only 1 S. cinereus was captured during the study (in 1979). Three trap periods were completed in each of the 12 areas in 1978: 1) 30 May to 29 June, 2) 30 June to 2 August, 3) 3 August to 7 September. In 7200 trap days in 1978, 80 individuals of the 3 microtine species were captured on the 12 grids in the 30-ha study plot: 59 L. sibericus, 11 D. torquatus, and 10 M. oeconomus. Recaptures were rare between periods, although they were frequent within a period; there were 127 total captures of the 80 individuals. That only 7 individuals were captured in more than one period was due to the combined effects of short life span and a long interval between trap periods. Between 2 and 17 captures occurred in each of the 12 grids in 1978, and the ratio of successful to unsuccessful trap locations was 88/1200 (0.073).

Ten trap periods were completed in 1979:

1) 30 May to 15 June
2) 16 to 22 June
3) 23 June to 2 July
4) 3 to 12 July
5) 13 to 22 July
6) 23 July to 1 August
7) 2 to 11 August
8) 12 to 21 August
9) 22 to 31 August
10) 1 to 7 September.

In 10,900 trap days only 33 individuals of the 3 microtine species were captured in all trap areas combined: 18 L. sibericus, 6 D. torquatus, and 9 M. oeconomus. Trap mortality was higher in 1979

due to the longer period between trap checks and frequent sunny weather. Ten animals (5 females) died in traps during 1979, but only 4 trap deaths (all males) occurred in 1978. Seven animals were captured in at least 2 trap periods and 1 individual survived at least 7 trap periods. Trap areas 4 and 11 on the 30-ha plot were the only 100-trap grids in which any captures were made in 1979; 17 and 27 captures were made in areas 4 and 11, respectively. Forty-six captures were made on the dozer transect (including 25 captures on area 11 which were within 20 m of the trail). Twelve captures were made in small quadrats, 4 of which were on the 30-ha study plot. Thus, 33 individuals were captured 77 times in 1979. The ratio of successful to unsuccessful trap sites was 38/668 (0.057). This is a decrease from the previous year, indicating that the efficiency of the trap effort was not increased by concentration on identified preferred vegetation types. Captures in 1979 were limited almost exclusively to sites at which captures occurred in 1978 (Figs. 4, 5, and 6).

M. oeconomus occurred only in area 4, and within that grid was restricted to traps in Dupontia meadow. No other populations of M. oeconomus were located in the study area. Most of the Dupontia meadow was flooded during breakup for several days or weeks each spring and in both years the population began the season with very few animals, possibly immigrants. Little evidence of winter use of this area was noted in early spring of either year and wintering areas were not conspicuous. Other researchers have documented a seasonal shift

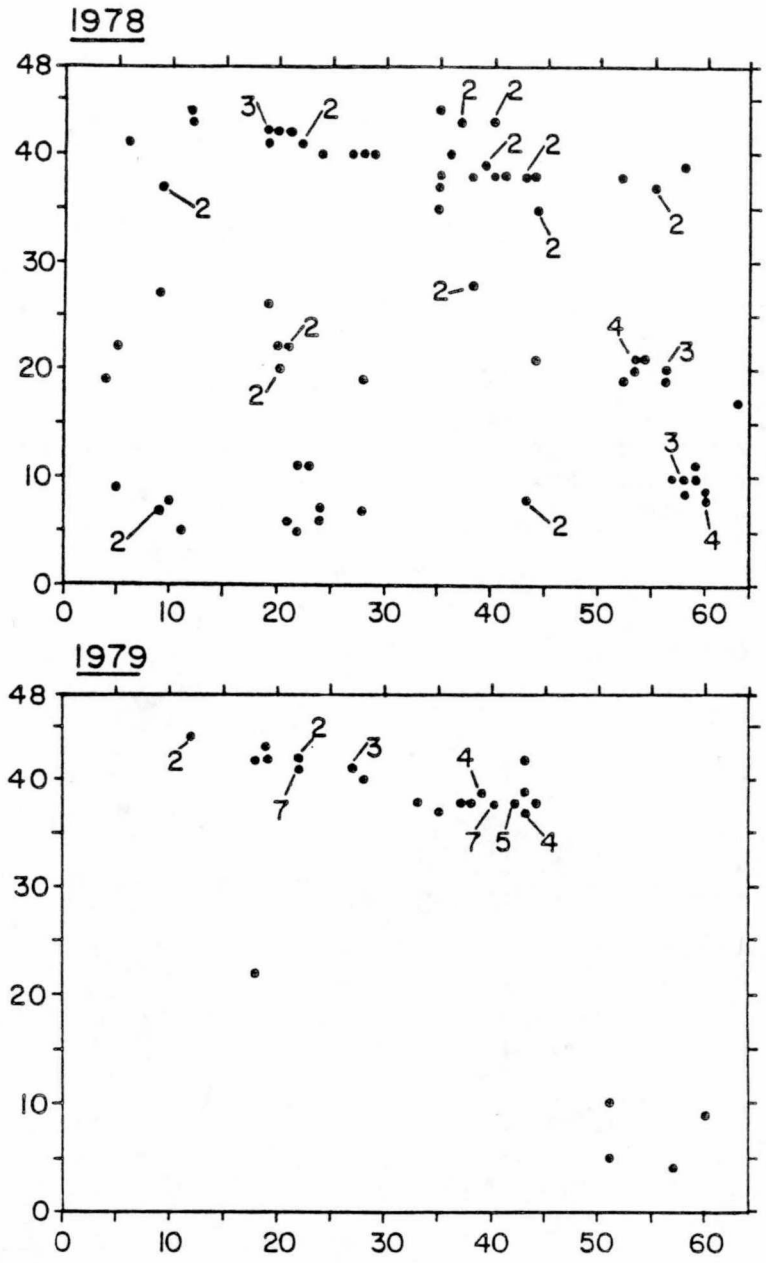

Figure 4. Map of 30-ha study plot showing capture sites of L. sibericus in 1978 and 1979 at Demarcation Bay, Alaska. Coordinates are in 10-m intervals.

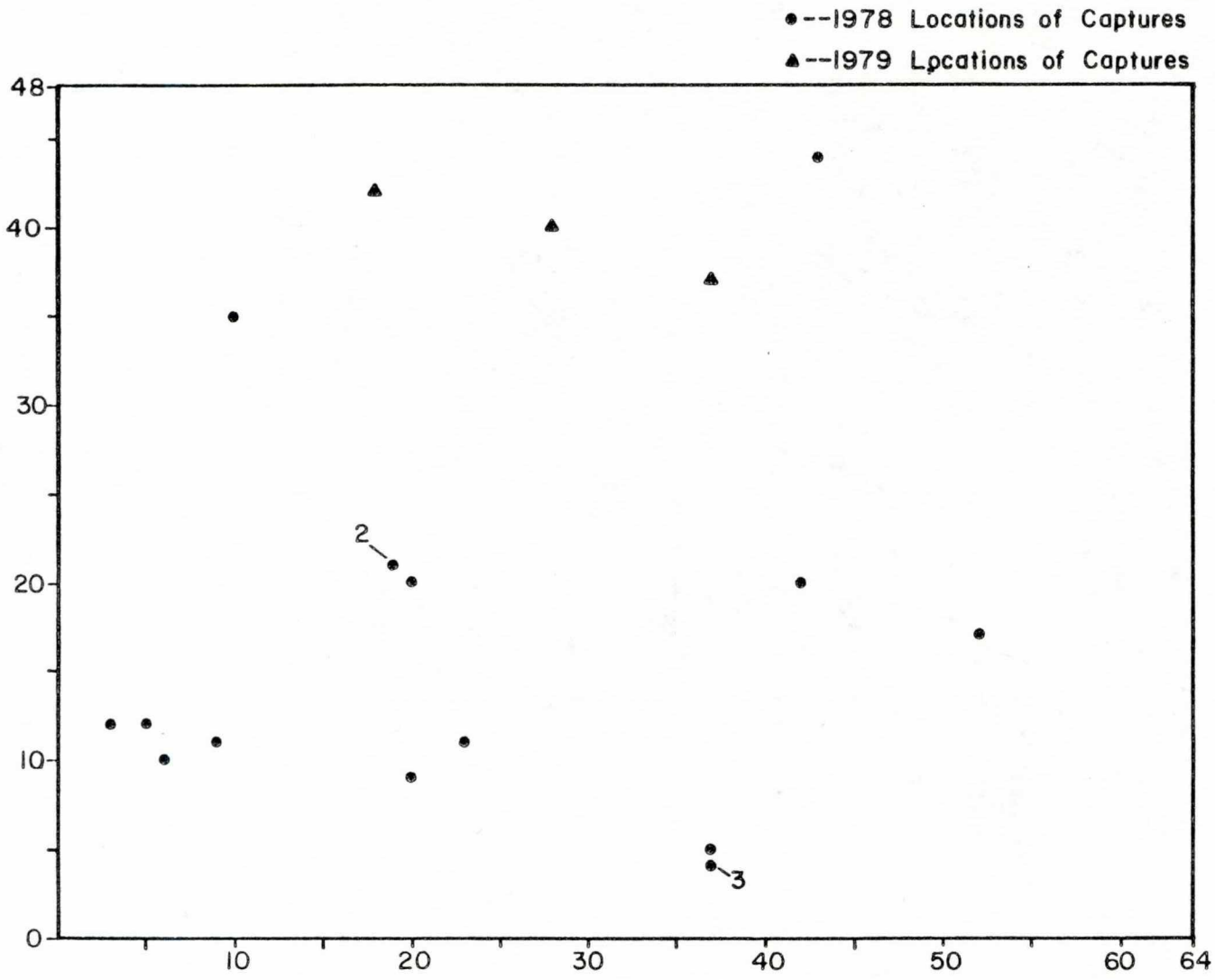

Figure 5. Map of 30-ha study plot showing capture sites of D. torquatus in 1978 and 1979 at Demarcation Bay, Alaska. Coordinates are in 10-m intervals.

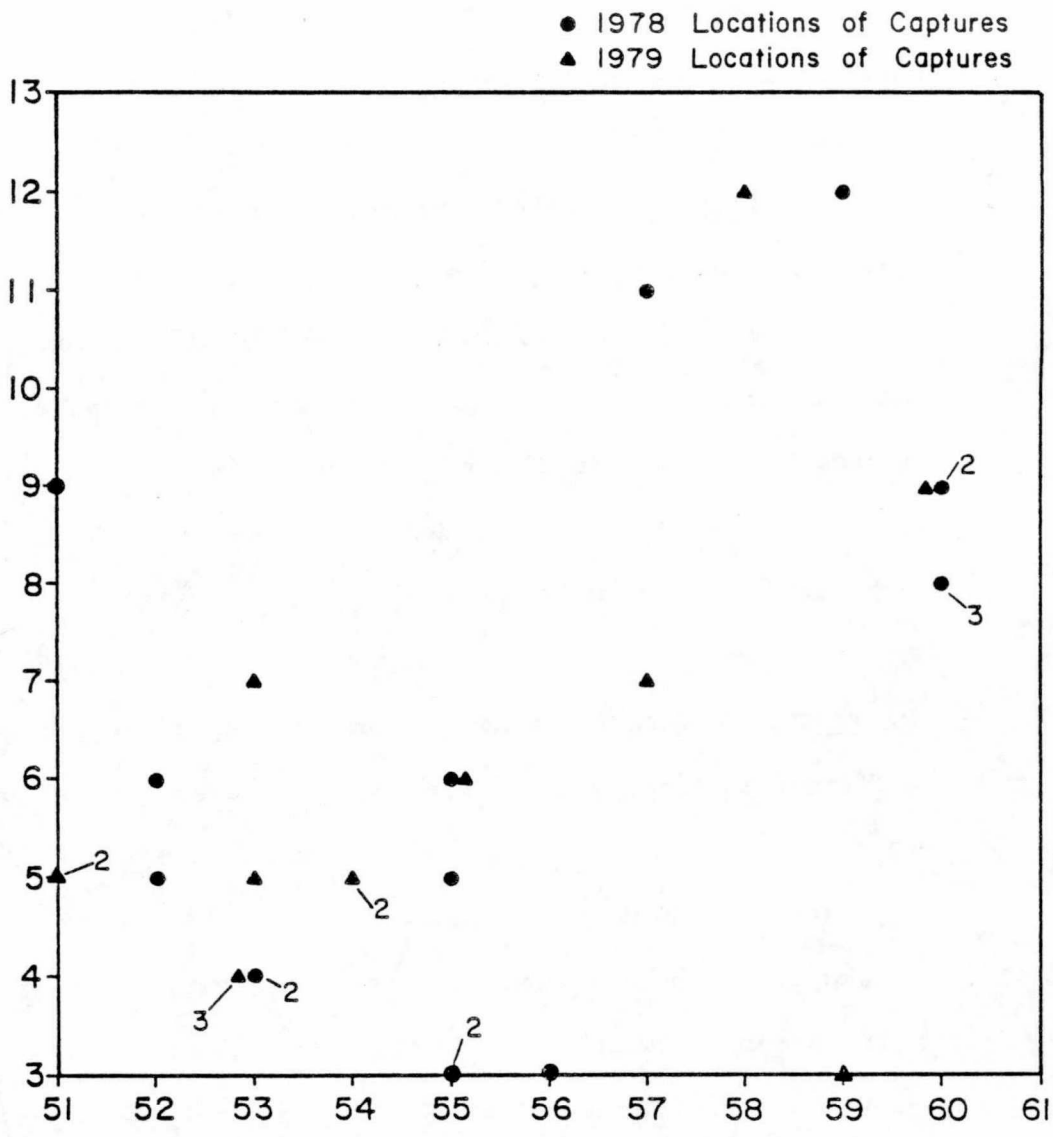

Figure 6. Map of 100-trap grid number 4 in the 30-ha study plot showing capture sites of M. oeconomus in 1978 and 1979 at Demarcation Bay, Alaska. Coordinates are in 10-m intervals.

in habitat use by M. oeconomus in northern Europe (Tast 1966, Kostian 1970) and a similar phenomenon appears to occur here.

L. sibericus were most numerous in areas 4, 5, and 11, but their distribution and abundance changed as ice and water receded on areas 11 and 5 and as M. oeconomus density increased on area 4.

L. sibericus densities were greater in the dozer trail than in any other vegetation types sampled in both years. In the following summary, traps within 20 m of the trail in either year are treated as part of the dozer transect. There were 124 traps on the dozer transect (i.e. within 20 m of the trail) from trap areas 9, 10, and 11 in 1978 and 83 traps on the dozer transect in 1979. During 744 trap days in 1978, 17 individuals of L. sibericus were captured on the dozer transect; during 1660 trap days in 1979, 13 L. sibericus and 2 D. torquatus were captured. Although trap placement was somewhat different in the 2 years, density of successful traps was highest in the dozer trail in both years, as shown in Fig. 4. The spring population of both years was composed of large adults. During breakups, the mounds were the only dry ground in the area and were refuges for overwintered animals of both lemming species. In both years the early summer population in the dozer mounds was substantially lower than in spring, although younger animals appeared in summer samples. The decrease was probably due to dispersal from the mounds as the surrounding tundra dried. However, only one instance of dispersal from the dozer trail was documented; a large adult male L. sibericus moved from the trail in area 11 to area 5,

then to area 4 before disappearing. Seasonal shifts of habitat use for L. sibericus have been documented by Batzli (1975).

No local population centers of D. torquatus were located in the study area. Although present, individuals were dispersed. Five of 11 D. torquatus were in tussock slope and high center polygons in areas 1 and 2 during 1978. During 1979, 2 captures occurred in the dozer transect, 2 in high relief lcp and 2 in high center polygons.

II. DISCUSSION

A. Trappability

Trappability (as measured here) is the probability that a marked animal present on the trap grid will be re-captured in a given trap period. Estimates of trappability have 2 uses: 1) as indices to the success of the trap effort and the reliability of density estimates, and 2) to examine individual or group differences in reaction to traps. The magnitude of the estimate of trappability depends on both methodological and biological factors including: quality of traps, trap distribution and number relative to population density, type of bait, behavioral reactions of animals to traps, social behavior, and activity. Trappability is calculated as the total catch in a period divided by the number known alive at that trapping from trap records (Boonstra and Krebs 1978). This is not the same as the probability of capture of an unmarked animal and the estimate tells nothing about the unmarked population.

In 1978, data were collected for 3 widely-spaced trap periods, with low survival between periods. No estimate of trappability between periods was possible. Recaptures were more common with a 10-d interval between trap periods in 1979 and data for calculation of trappability are presented in Table 3. The average trappability in 1979 was 0.899, indicating that approximately one marked animal in 10 escaped capture in any trap period. This compares favorably with other estimates of average trappability of microtine rodents, which ranged from 0.53 to 0.99 (Boonstra and Krebs 1978, Cole and Batzli 1978, Getz et al. 1979, Beacham and Krebs 1980).

Dividing trap periods into 24-h intervals for calculation of trappabilities reduces the absolute value of the estimate (due to lower probability of capture in a shorter time interval) but allows comparison between sex and age/weight groups and between years. Age/weight classes for L. sibericus (from Batzli 1975) are: juveniles, $\leq$28 g; subadult females, 29-39 g; subadult males, 29-44 g; adult females, $\geq$40 g; adult males, $\geq$45 g. Age/weight classes for D. torquatus (adapted from those for L. sibericus) are: subadults, $\leq$30 g; adults, >30 g. Age/weight classes for M. oeconomus (from Whitney 1976) are: juveniles, $\leq$17 g; subadults, 18-25 g; adults, $\geq$26 g. No significant differences ($p>0.05$) in number of captures were found between day 1 and day 2 of each trap period, justifying the use of 24-h periods. No differences in mean 24-h trappabilities of each sex/age group were found between years ($p>0.05$); with years combined no differences were found between sexes of each age group. With years

Table 3. Ten-day period estimates of small mammal trappability at Demarcation Bay, Alaska in 1979, all species pooled.

	10-day periods									
	1	2	3	4	5	6	7	8	9	10
Catch	7	7	4	5	3	5	7	2	5	6
Total Known Alive	7	8	5	5	4	5	7	3	5	6
Proportion Captured	1.00	0.87	0.80	1.00	0.75	1.00	1.00	0.67	1.00	1.00

Trappability (average proportion captured periods 2 through 10)= 0.90
(SD= 0.131)

and sexes combined, no differences were found in average trappability between age groups of each species. Average 24-h trappabilities were 0.71 (SD=0.40, n=21 24-h periods), 0.62 (SD=0.26, n=26),and 0.53 (SD=0.30, n=14) for M. oeconomus, L. sibericus and D. torquatus, respectively. No significant differences were found ($p>0.05$) between species.

Other studies have documented low juvenile trappability for microtines and have concluded that the most trappable individuals are those dominant in the social structure of the population (Gliwicz 1970, Hilborn et al. 1976). There are 2 possible explanations for the lack of a significant difference in average trappability between age groups in this investigation. First, the total number of animals known alive in any 24-h period was consistently small (range 0 to 7) and, therefore, yielded a bimodal distribution of trappability estimates. Second, low density populations of all 3 species reduced both the level of trap competition (indicated by the ratio of numbers of individuals to the number of traps) and the number of social encounters between adults and juveniles. Either factor could act to increase the trappability of marked juveniles to near adult levels. Trappability has been shown to increase in microtine populations as density decreases (Boonstra 1977, Boonstra and Krebs 1978, Cole and Batzli 1978, Beacham 1979).

In spite of the high trappability exhibited by juveniles after the first trap experience, few animals were first captured as juveniles. This is an indication that trappability differed between

marked and unmarked animals. Assuming that animals weighing less than 40 g at first capture originated on the plot, the average weight at first capture of L. sibericus (under 40 g) was 33.3 g (n=43). Assuming animals captured after period 1 and weighing less than 40 g at first capture were resident during previous trap periods in 1979, only 30% (3/10) first entered a trap at a juvenile weight ($\leq$28 g). The underrepresentation of juveniles in trap records appears to be common to microtine investigations where box-type live traps are used (Boonstra and Krebs 1978), leading Hilborn et al. (1976) to recommend separate estimation of juvenile numbers.

In conclusion, analysis indicates that trap methods yielded overall trappability (0.9) in 1979 comparable to other microtine trapping efforts. Comparisons of average 24-h trappabilities revealed no differences between age/weight groups, sexes, years or species. However, this was attributed to the small number of animals known alive in any 24-h period and subsequent large variance among the 24-h estimates of trappability. The low number of juveniles in the trap records and the high average weight at first capture are probably the result of low trappability of unmarked juveniles.

B. Density

The calculation of density requires the estimation of effective trap area. Two groups of methods are available: 1) probabilistic techniques, such as those which rely on the distribution of captures from outer to inner grid stations (O'Farrell et al. 1977, Hansson

1979), and 2) boundary strip techniques, where the width of the strip added to the trap grid area equals the average distance moved between captures (Brant 1962, Lidicker 1966, Flowerdew 1972). The trap techniques used here and the low number of captures indicate use of the latter.

Recapture distances present several problems in analysis because of lack of independence between observations, and a non-normal and non-continuous distribution. In addition, the most long-lived animals and animals with high trappability contribute a disproportionate number of recaptures to a simple average. Therefore, means for each sex and age group of each species were calculated from average recapture distances for each individual. The distribution of mean values may also be non-normal, but is continuous and observations are independent.

Movements representing changes in home range use are eliminated by excluding from analysis all recaptures made at intervals of greater than 120 h. A total of 60 recaptures remained, representing 35 individuals: 28 L. sibericus, 3 D. torquatus and 4 M. oeconomus. Average recapture distances for sex and age groups of each species are presented in Table 4.

For D. torquatus and M. oeconomus, recaptures were too few for testing between years or age/sex groups. Average recapture distances of 36.85 m and 41.57 m were computed from all recaptures of D. torquatus and M. oeconomus, respectively.

Table 4. Recapture distances (m) for sex and age groups of 3 species of small mammals at Demarcation Bay, Alaska in 1978 and 1979. Recaptures at greater than a 120-h interval are excluded. Age/weight categories for L. sibericus are from Batzli (1975); those for D. torquatus are adapted from categories used for L. sibericus; and those for M. oeconomus are from Whitney (1976).

	1978			1979			Total		
	mean	(SD)	n	mean	(SD)	n	mean	(SD)	n
Lemmus sibericus									
Juvenile (≤28 g)	10.0	(14.14)	2	0.0	(0.00)	3	4.0	(8.94)	5
Subadults:									
males (29-44 g)	6.3	(7.40)	4	-	-	0	6.3	(7.40)	4
females (29-40 g)	-	-	0	11.8	(2.08)	2	11.8	(2.08)	3
Adults:									
males (≥45 g)	14.2	(20.68)	5	117.7	(6.43)	2	*		
females (≥40 g)	18.1	(19.34)	8	0.0	(0.00)	1	16.1	(19.07)	9
Total (excluding adult males in 1979)							11.4	(15.13)	26
Dicrostonyx torquatus									
Subadults: (≤30 g)									
males	-	-	0	-	-	0	-	-	0
females	-	-	0	-	-	0	-	-	0
Adults: (>30 g)									
males	-	-	0	98.5	(0.00)	1	98.5	(0.00)	1
females	6.0	(1.45)	2	-	-	0	6.0	(1.45)	2
Total							36.8	(53.40)	3
Microtus oeconomus									
Juvenile (≤17 g)	-	-	0	-	-	0	-	-	0
Subadults: (18-25 g)									
males	-	-	0	-	-	0	-	-	0
females	-	-	0	-	-	0	-	-	0
Adults: (≥26 g)									
males	41.2	(0.00)	1	46.5	(0.00)	1	43.8	(3.75)	2
females	39.3	(25.46)	2	-	-	0	39.3	(25.46)	2
Total							41.6	(15.09)	4

* Indicates significant difference between years.

Adult male L. sibericus in 1979 moved significantly farther between captures than they did in 1978 (Mann-Whitney, $p<0.05$). No difference between years was detectable in the distribution of recapture distances of juveniles. Data were insufficient to compare years for other age/sex groups of L. sibericus. Years were combined for all age/sex groups except adult males and a test of distributions of recapture distances of the resulting 6 groups rejected the hypothesis that all were similar (Kruskal-Wallis, $p<0.05$). Although significance values in subsequent tests are distorted, pairwise tests indicated that only 1979 males differed from other age/sex groups.

Average recapture distance for adult male L. sibericus in 1979 was 117.7 m. Average recapture distance for other L. sibericus was 11.4 m. The average for adult males in 1979 was computed from 10 recaptures of 2 large overwintered animals in periods 1 to 7. One of these males was first captured as a juvenile in August 1978. The other weighed 60 g and was also probably an overwintered adult. A possible explanation for the greater recapture distances of these 2 males is the low density of the population. The higher density of large adult males in 1978 may have limited movements of all males through social interaction. In 1978, 13 adult males were captured, 5 of these were recaptured within 120 h of release and yielded a total of 6 recapture distances ranging from 0 to 50 m. Only 3 adult males were captured in 1979; the 10 recaptures of 2 of these individuals ranged from 14.1 to 210.2 m.

Increased movements and/or larger home ranges at low densities have been reported for adult males of L. sibericus, D. torquatus and several Microtus species (Getz 1961, Krebs 1966, Brooks and Banks 1971, Banks et al. 1975, Boonstra 1977). The summer reproductive strategy of most microtines, in which females are induced ovulators, involves dominant males visiting reproductive females every few days. At low densities males may be forced to move greater distances in search of mates.

Comparable estimates of recapture distances from the literature are unavailable for these species. On his 0.25-ha plots, Feist (1975) used boundary strips equal to one-half the average range length determined by Brooks and Banks (1971) through radiotracking D. torquatus at Churchill, Manitoba, Canada. The boundary widths were: 14 m for females obviously near term; 60 m for all other females; 14 m for subadult and juvenile males; and 134 m for adult males. Brooks and Banks (1971) also showed a distinct increase in male home range size of D. torquatus at lower population density, ranging from 0.6 ha (SD=0.15) at high density to 6.0 ha (SD=3.47) at low density. In a similar study of L. sibericus, Banks et al. (1975) found male home ranges, which averaged 1.3 ha, to vary little in relation to density, although males were found to be more active at lower densities. The average recapture distances found here for L. sibericus appear to be similar to those found by Brooks and Banks (1971) for D. torquatus and to show similar trends.

Effective trap areas calculated by adding a boundary strip equal in width to the average recapture distance are: 10.6 ha for L. sibericus adult males in 1979, 1.3 ha for other L. sibericus, 2.7 ha for D. torquatus, and 3.0 ha for M. oeconomus. Density estimates for each 100-trap grid are presented in Table 5.

Grids 1, 2, 3, 5, 6, 8, and 12 were sampled with 20 small quadrats in 1979. These 80 traps made no captures, yielding an estimate of 0 density (in animals per ha) for those areas of the study plot in 1979. Densities of L. sibericus and D. torquatus on the entire study plot averaged 1.4 (SD=1.48) and 0.1 (SD=0.22) animals per ha, respectively, in 1978 and 0.4 (SD=0.81) and <0.1 (SD=0.09) animals per ha, respectively, in 1979. The limited distribution of M. oeconomus did not warrant calculation of density over a larger area than grid 4 where their densities were similar each year, averaging 1.2/ha (SD=1.26) in 1978 and 1.2/ha (SD=1.01) in 1979.

The overall densities of L. sibericus and D. torquatus decreased between 1978 and 1979 on all trap areas. Densities increased significantly each summer only on area 11. The general increase in densities of L. sibericus in most areas in 1978 was the result of increased dispersion rather than increased numbers. Overall density of L. sibericus decreased through the summer in 1979; females were present only on areas 10 and 11 and increased density occurred only on the latter area. Decreased densities from period 1 to 2 on areas 10 and 11 were probably the result of concentration in the dry mounds of

Table 5. Small mammal densities (animals/ha) on 100-trap grids at Demarcation Bay, Alaska in 1978 and 1979.

Area	*L. sibericus*			*D. torquatus*			*M. oeconomus*		
	period 1	period 2	period 3	period 1	period 2	period 3	period 1	period 2	period 3
1978									
1	0.79	0.79	1.57	0.75	0.75	0.0	-	-	-
2	1.57	0.79	1.57	0.0	0.37	0.37	-	-	-
3	0.0	0.0	0.79	0.0	0.37	0.37	-	-	-
4	2.36	3.15	0.79	-	-	-	0.33	0.67	2.67
5	1.57	3.94	1.57	0.37	0.0	0.0	-	-	-
6	0.79	0.0	0.79	0.37	0.0	0.0	-	-	-
7	0.0	0.0	2.36	0.37	0.0	0.0	-	-	-
8	0.0	0.0	2.36	-	-	-	-	-	-
9	0.79	1.57	0.79	0.37	0.0	0.0	-	-	-
10	3.94	0.79	0.79	-	-	-	-	-	-
11	3.94	1.57	7.09	0.37	0.0	0.0	-	-	-
12	0.79	1.57	0.79	-	-	-	-	-	-
ave.*	1.34	1.18	1.77	0.22	0.12	0.06			
(SD)	(1.42)	(1.28)	(1.78)	(0.25)	(0.24)	(0.14)			
1979									
4	0.87	0.87	0.09	-	-	-	0.33	1.00	2.33
7	0.00	0.00	0.78	-	-	-	-	-	-
9	0.87	0.0	0.0	-	-	-	-	-	-
10	2.55	0.09	0.0	0.37	0.0	0.0	-	-	-
11	1.66	2.45	3.15	0.37	0.0	0.0	-	-	-
13	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-
ave.	0.85	0.49	0.57	0.11	0.0	0.0			
(SD)	(0.98)	(0.92)	(1.17)	(0.18)					

* Average is for all trap areas combined. No average is presented for *M. oeconomus* due to its limited distribution in the study area.

the dozer trail during breakup and subsequent dispersal when breeding began.

D. torquatus was not abundant in either year, but disappeared entirely from the trap grids after period 1 in 1979. In 1978, dispersion increased from early to late summer. This is likely the result of dispersal from drier 'refuge' habitats occupied during breakup.

In both years M. oeconomus density on area 4 increased gradually throughout the summer. Although seasonality of habitat use has been implicated in affecting densities, M. oeconomus did not utilize the dozer mounds as a refuge during breakup as did the lemmings. Seasonal habitat use patterns of M. oeconomus differ from other species in that summer habitats are often flooded throughout winter and winter habitats may be 3 to 200 m from summer habitats (Tast 1966, Kostian 1970). The winter habitat of this population was apparently off the study plot. The increase in numbers of M. oeconomus on area 4 was accompanied by a decline in use of the area by L. sibericus (Fig. 7). Early season densities of L. sibericus, before influx of voles, were comparable to those in preferred vegetation types and their subsequent decline may be attributable to interaction with voles. Other studies have found M. oeconomus capable of excluding L. sibericus from preferred habitat where their ranges overlap (Rausch and Rausch 1975).

The density of small mammals on the 30-ha study plot is not representative of the study area for 2 reasons: 1) differences in the distributions of vegetation types in the plot and the study area, and

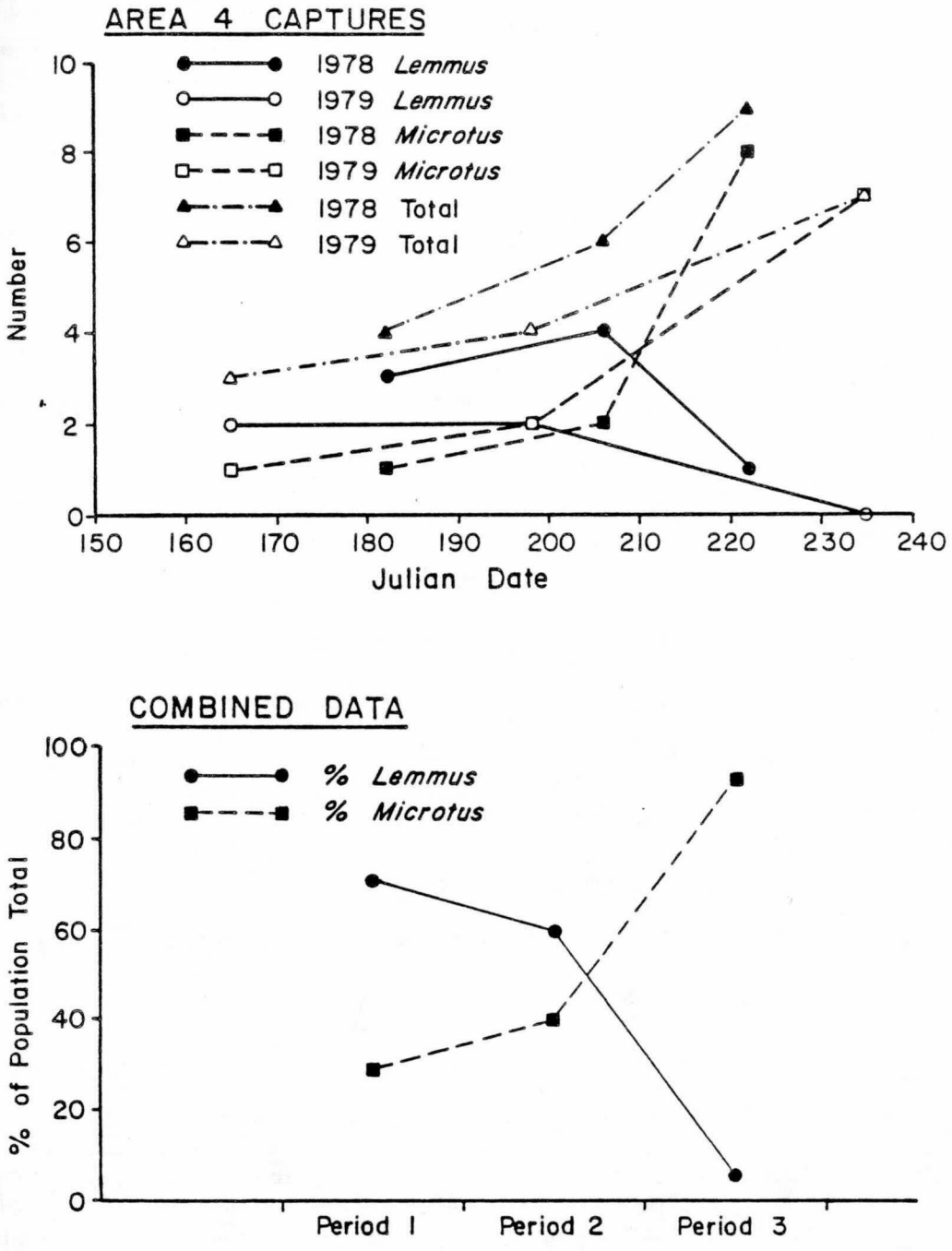

Figure 7. Population trends of L. sibericus and M. oeconomus on 100-trap grid number 4 at Demarcation Bay, Alaska. Upper graph shows number of captures in each trap period for each species in each year. Lower graph illustrates the proportion of captures of each species in the combined years catch for each trap period (1979 data are presented in 3 intervals comparable to the 1978 trap periods).

2) a patchy distribution of small mammal populations both within and between vegetation types. Although small mammal sign was abundant in L. sibericus and M. oeconomus habitats on the study plot, sign was rare in other parts of the study area. Captures of small mammals by foxes were uncommon (see Arctic Fox Investigations, Section II, G). Several of the captures which were observed occurred on the study plot. Therefore, extrapolation of densities to the entire study area over-estimates the availability of small mammal prey to foxes.

C. Demography

Mean survival of marked animals was calculated by tallying the number surviving and the number disappearing from the populations each trap period, summing over all periods and dividing by the number of periods. Mean survival rates are based on sums of samples which are not independent and hence no statistical comparisons are made.

Death and emigration were not individually assessed in this study and both factors influence the survival estimates. It is not known to what extent the decreases in density which occurred in some periods were due to emigration. Few instances of a long distance movement or home range shift appear in the capture data. Most animals simply disappeared between trap periods. Perhaps dispersing individuals are not attracted to traps and/or marked dispersers are rarely retrapped. Whatever the case, death and emigration are not separated here.

Estimates of survival in this study suffer from small numbers and long intervals between trap periods. Ten-day survival of marked

animals in 1979 was estimated as 0.68, which would appear to be very poor survival. Trap periods were less frequent in 1978 and only 30-d survival can be compared between years: 0.23 in 1978 and 0.33 in 1979. Data were too limited for age or sex group comparisons. These are minimum estimates of survival and are significantly affected by the possibility of a marked animal not appearing in a late summer sample. Such low survival has been documented in cyclic species during population crashes by Chitty and Phipps (1966). However, the data presented here are limited and such comparisons must be made with caution.

Survival of juveniles is typically lower than that of adults for most microtine species. The juvenile period is divided into suckling (0 to 15 d) and weanling (15 to 28 d) in L. sibericus (Collier et al. 1975). Suckling survival was found to be between 0.48 and 0.58 per 12 d in L. sibericus by Batzli et al. (1974). Manning (1954) reported mortality in D. torquatus age 0 to 8 d as approximately 0.33. Most studies indicate that suckling survival is typically higher and less variable than weanling survival, which is quite variable. Batzli et al. (1974) found mortality of L. sibericus to be highest in the first 2 weeks after weaning.

Survival of sucklings and weanlings cannot be computed from mark-recapture data. However, it is possible to calculate an index to survival of animals from birth to trappable age by comparing the estimated number of births at time t (from data on pregnancies in marked females) to the number of new animals entering the trapped

population at time t+A, where A is the approximate age at first capture. Calculation of this index requires estimates for: 1) average litter size, 2) age at first capture, and 3) number of pregnant females in the population. Capture data necessary for estimates are presented in Table 6. The methods used to calculate each estimate are presented in Appendix 4.

The total number of animals estimated to have been born on the plot during the study was 17 in 1978 and 7 in 1979. The total number of births before the final trap period, based on reproductive records of females, was 30 in 1978 and 15 in 1979. However, Table 6 shows new animals appearing in the population in both years which could not be assigned to a known pregnancy. There are 2 likely explanations. One is that many females had probably reached reproductive age before entering traps. The approximate mean age at first capture of females in this study was 27.9 d (calculated from average weights using methods described in Appendix 4). Many microtines are capable of reproducing at a very low weight. Rausch and Rausch (1975) reported a pregnancy in a 14-d old weanling L. sibericus. In addition, the long interval between some captures in 1979 and between all trap periods in 1978 probably prevented detection of some pregnancies. Pregnancies cannot be determined accurately by external examination unless the animal is near term and visibly gravid. With frequent captures, weight fluctuations in females over 28 g were assumed to be due to pregnancies. However, in 1978 the interval between trap periods was longer than the gestation periods of 19 to 21 d reported for

Table 6. Measures of productivity of small mammals at Demarcation Bay, Alaska in 1978 and 1979.

Period	Number of pregnant females[1]	Estimated number of births[2]	Number of unmarked animals[1]	Estimated births of unmarked animals[3]	Total number of females[1]	Proportion of females pregnant
1978						
L. sibericus[4]						
1a	4	20	-	2	10	0.40
1b	-	-	-	12	-	-
2a	2	10	4	13	5	0.40
2b	-	-	-	0	-	-
3a	1	5	23	-	4	0.25
D. torquatus						
1	1	5	-	*[5]	4	0.25
2	0	0	2	*	1	0
3	0	0	0	*	1	0
M. oeconomus						
1	0	0	0	*	0	-
2	0	0	1	*	2	0
3	1	5	1	*	2	0.50
1979						
L. sibericus						
1	0	0	-	1	0(1)	0
2	1(2)	5	0	3	2(3)	0.67
3	0	0	0	0	0	-
4	0	0	1	0	0	-
5	0	0	1	2	1	0
6	0	0	2	0	2	0
7	0	0	1	0	2	0
8	0	0	0	1	2	0
9	2	10	2	0	2	0.67
10	0	0	0	-	2	0
D. torquatus						
2	0	0	1	*	1	0
3	2	10	0	*	2	1.00
4	0	0	1	*	1(2)	0
M. oeconomus						
6	0	0	1	*	0	-
7	0	0	1	*	1	0
8	1	5	1	*	1	0
10	4	20	4	*	4	1.00

[1] From trap records; trap deaths (in parentheses) excluded.
[2] From average litter size of 5, see Appendix 4.
[3] Dates of birth extrapolated from weight using growth equations given in Appendix 4.
[4] Because the interval between trap periods in 1978 is longer than the gestation period of L. sibericus, births are assigned to 2-week periods within each trap period (see Appendix 4).
[5] * indicates too few captures to estimate.

L. sibericus and D. torquatus (Manning 1954, Mullen 1968, Rausch and Rausch 1975). For this reason births in the 2-week interval before each trap period in 1978 were probably undetected. At the low population levels encountered in this study, a single missed pregnancy substantially reduces estimates of productivity and juvenile survival.

The second factor which may be responsible for the appearance of animals not attributable to a known pregnancy is immigration. Movements of over 100 m within the 30-ha plot were limited to large adult males. However, if unmarked animals, particularly juveniles, show increased dispersal tendency, or if dispersers have lower trappability, the assumption that unmarked animals less than 40 g originated on the plot may be violated too frequently for calculation of a valid index to juvenile survival.

In spite of these difficulties, Table 6 indicates definite decreases in productivity and juvenile survival from 1978 to 1979 in L. sibericus. The 1979 population was very unproductive, with a very low incidence of pregnancies and few juveniles and subadults appearing in the mid- to late summer population. In contrast, the proportion of females pregnant averaged higher in each trap period in 1978 and a large number of animals entered the population in mid- to late summer. The ratio of new captures to estimated births in periods for which pregnancies were documented is 15/30 in 1978 and 3/15 in 1979 (Table 6), in spite of the shorter interval between trap periods in 1979. This is fairly strong evidence of a real difference in juvenile survival between years.

Comparisons of weight distributions also indicate between year differences in demography. Average weights per period are presented in Table 7. Pregnant females were excluded from the calculations. The 1979 data are presented in 3 periods comparable to 1978 periods. The weight distributions of period 1 in 1978 and 1979 L. sibericus were significantly different (Mann-Whitney, $p<0.05$). No significant differences in weight distributions between years were found in periods 2 or 3. No differences were found between years for D. torquatus or M. oeconomus.

Age/weight distributions of L. sibericus are presented in Table 8. In 1978, L. sibericus weight distributions show a typical spring population composed predominantly of heavy adults; no juveniles appeared in the June sample. The mid-summer population was mixed, as is also shown by the higher variance in average weight (Table 7); the sample had 8 heavy adults, 3 subadults and 4 juveniles. In late summer only 2 of the trapped animals were over 40 g. This represents the typical yearly cycle for most seasonally reproductive microtines and is characteristic of a growing population (Batzli 1975).

The relative frequency of 5-g weight classes of L. sibericus in 1978 (Fig. 8a) shows a definite bimodal distribution. The heavy adults are mostly overwinter survivors, their cohort experienced very good survival through early summer. Few medium weight animals were present, indicating lack of winter reproduction and perhaps a lag in reproductive effort in early summer. The large number of animals under 35 g are probably members of 2 summer cohorts, as suggested by

Table 7. Average weights of each small mammal species captured at Demarcation Bay, Alaska for each trap period. Trap periods in 1979 are combined to yield 3 periods comparable to 1978 periods.

	1978			1979		
	period 1	per 2	per 3	per 1	per 2	per 3
Lemmus sibericus						
number	15	15	26	7	7	6
average weight	61.7	41.4	27.8	33.2	44.1	33.8
(SD)	(10.4)	(18.9)	(8.0)	(14.0)	(16.0)	(17.6)
Dicrostonyx torquatus						
number	6	4	2	4	2	0
average weight	44.2	33.5	38.0	45.2	27.5	--
(SD)	(12.8)	(15.0)	(14.1)	(11.3)	(2.1)	--
Microtus oeconomus						
number	1	4	7	2	3	3
average weight	26.0	31.0	34.2	45.0	39.4	39.0
(SD)	--	(8.4)	(6.3)	(2.8)	(17.8)	(5.6)

Table 8. Age/weight distributions of *Lemmus sibericus* captured in 1978 and 1979 at Demarcation Bay, Alaska. Age/weight categories are as defined in Table 4.

	Period 1		Period 2		Period 3	
	number	proportion	number	proportion	number	proportion
1978						
juvenile	0	0.00	4	0.27	13	0.50
subadult	0	0.00	3	0.20	12	0.46
adult	15	1.00	8	0.53	1	0.04
	15		15		26	
1979						
juvenile	3	0.43	1	0.14	2	0.33
subadult	2	0.29	4	0.57	3	0.50
adult	2	0.29	2	0.29	1	0.17
	7		7		6	

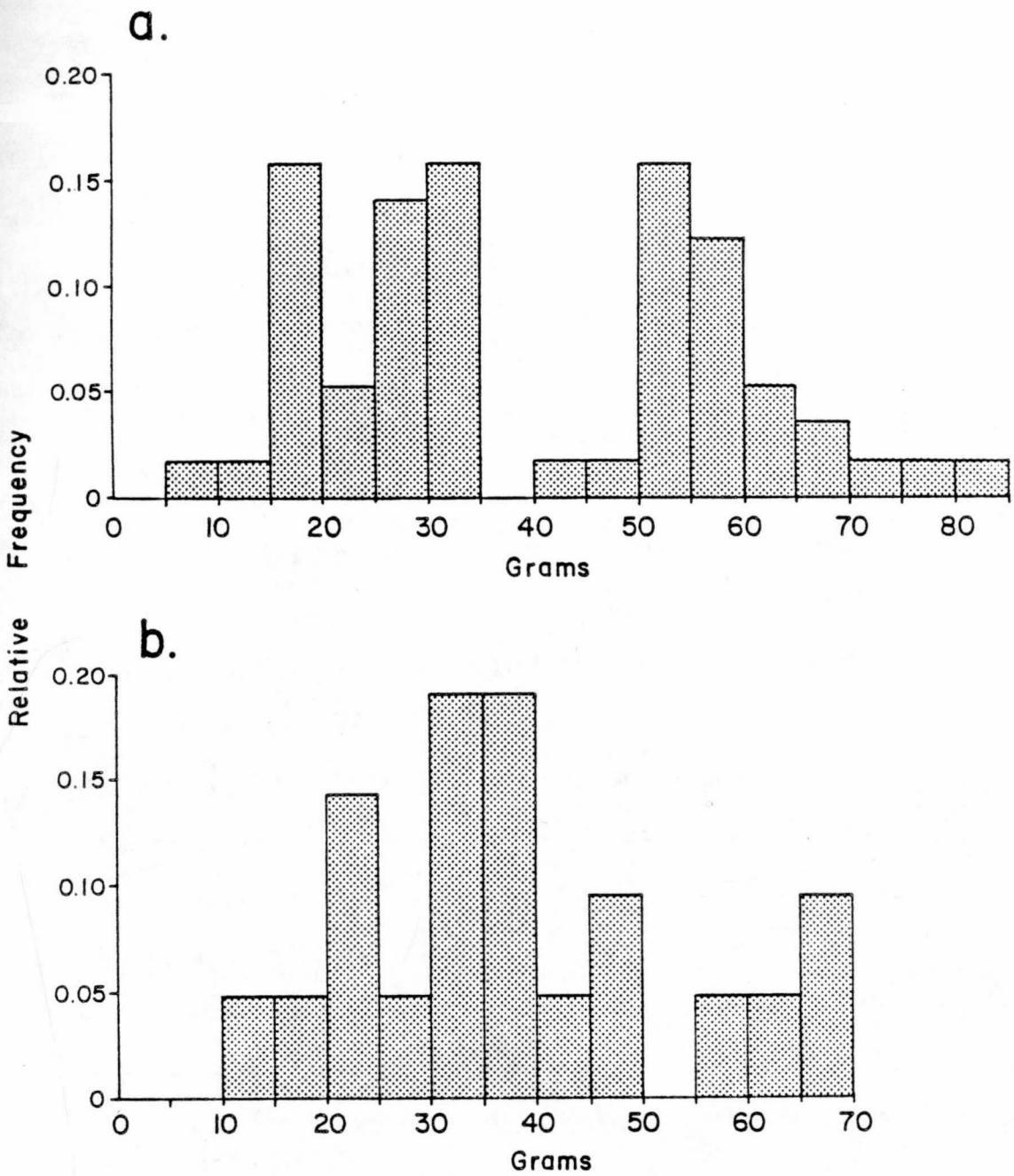

Figure 8. a. Relative frequency of 5-g weight classes of L. sibericus at Demarcation Bay, Alaska in 1978.
b. Relative frequency of 5-g weight classes of L. sibericus at Demarcation Bay, Alaska in 1979.

the bimodality in their weights. In addition, the cumulative frequency curve (Fig. 9a) is obviously affected by an extended period without reproduction, resulting in the large weight difference between overwintered animals and the first 2 summer cohorts. The cumulative frequency curve also provides an estimate of median ecological longevity: the value of age/weight when relative cumulative frequency equals 0.5, which is 34 g or 37 days. The relative cumulative frequency at any weight is an approximation to the probability of survival from appearance in the marked population to the attainment of that weight (Dapson 1971).

In 1979, juvenile L. sibericus appeared in the population in May. Approximately 60% of the catch weighed less than 40 g in the early samples. Adults in 1979 were neither as numerous nor as heavy as were adults in early summer 1978. Only one marked animal from the large August sample in 1978 survived to be trapped in spring 1979. However, the presence of juveniles and subadults in the spring 1979 sample indicate reproduction in late winter and early spring by overwintering animals. This suggests high mortality, possibly related to the early onset of reproduction, among heavy overwintered adults prior to the initiation of the trap effort. In 1979 both the mid-summer and late summer populations have weight distributions similar to that of the early summer population. This pattern of weight distributions is typical of a stable or declining population with mortality affecting all age classes similarly.

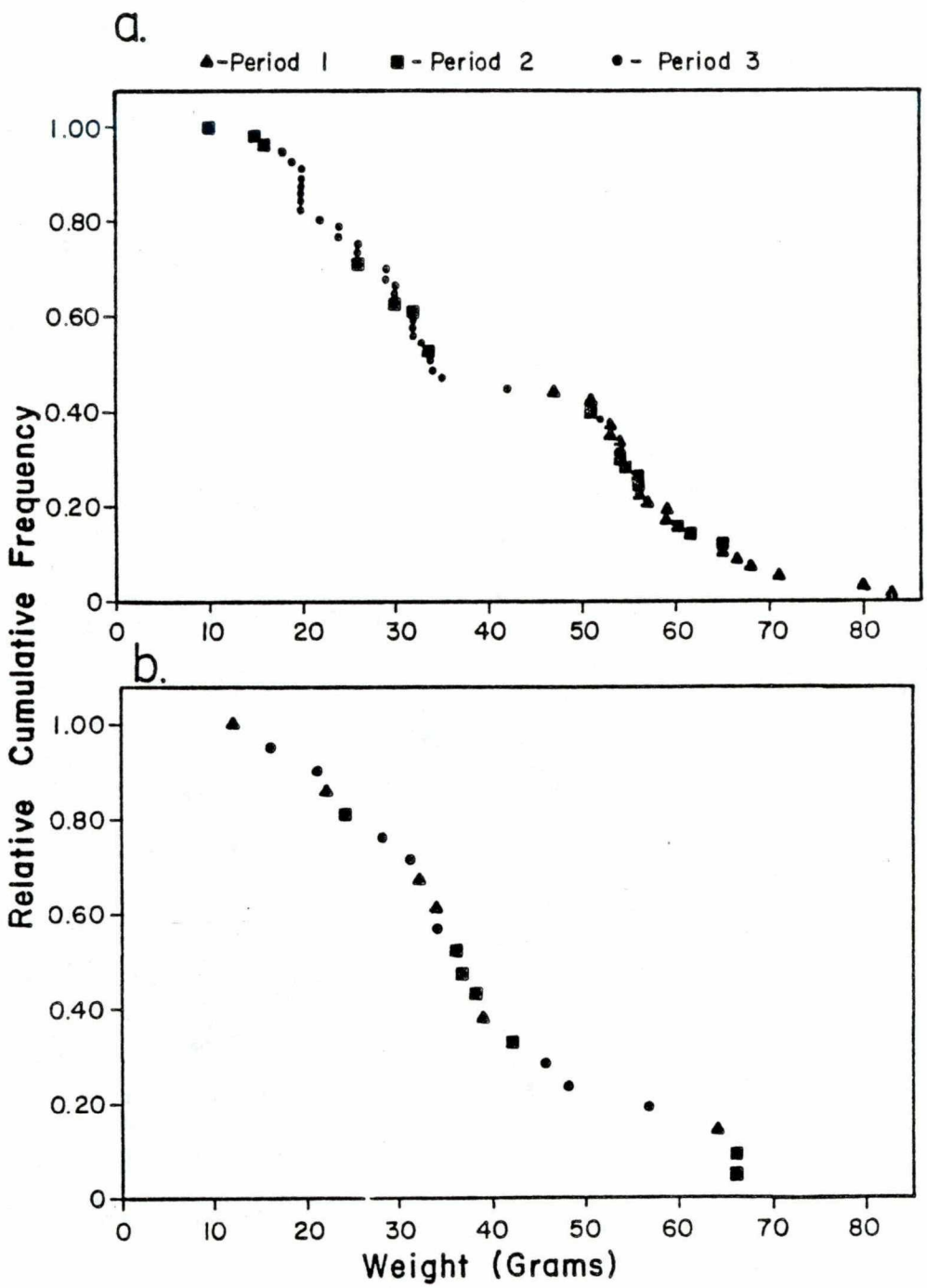

Figure 9. a. Relative cumulative frequency of weights of L. sibericus at Demarcation Bay, Alaska in 1978.
b. Relative cumulative frequency of weights of L. sibericus at Demarcation Bay, Alaska in 1979.

The graph of relative frequency of 5-g weight classes in 1979 (Fig. 8b) shows a uni-modal distribution with highest frequency in the middle weight classes, contrasting strongly with that for 1978. Heavy individuals experienced poor survival through spring and early summer. The predominance of the mid-weight class was due, in part, to late winter and early spring breeding. The cumulative frequency curve (Fig. 9b) is typical of a continuously reproducing stable or gradually declining population. Fig. 9 also indicates a slightly higher median ecological longevity in 1979 (36 g or 39 d) than in 1978. The distribution of weights was relatively even throughout the summer, with no surge of juveniles appearing in recognizable cohorts. The heavy individuals of the 1978 population have no counterpart in 1979; the large overwintered adults apparently were subject to unknown mortality before trapping began.

The difference in L. sibericus populations in spring 1978 and spring 1979 may have been due to environmental factors affecting the timing of reproduction. November and December 1978, and January, April, and May 1979 were warmer than usual; breakup in 1979 began in April and extended over a 2-mo period (Fig. 2). However, monthly weather data for late winter 1978 show that January, February, and March were particularly warm, and April was also above average (Fig. 2). The significant factor might have been the extended warm spell in late April and early May 1979 (Fig. 10) which did not occur in 1978. Quay (1960) found temperature to be the most significant variable affecting reproduction in D. torquatus and Mullen (1968)

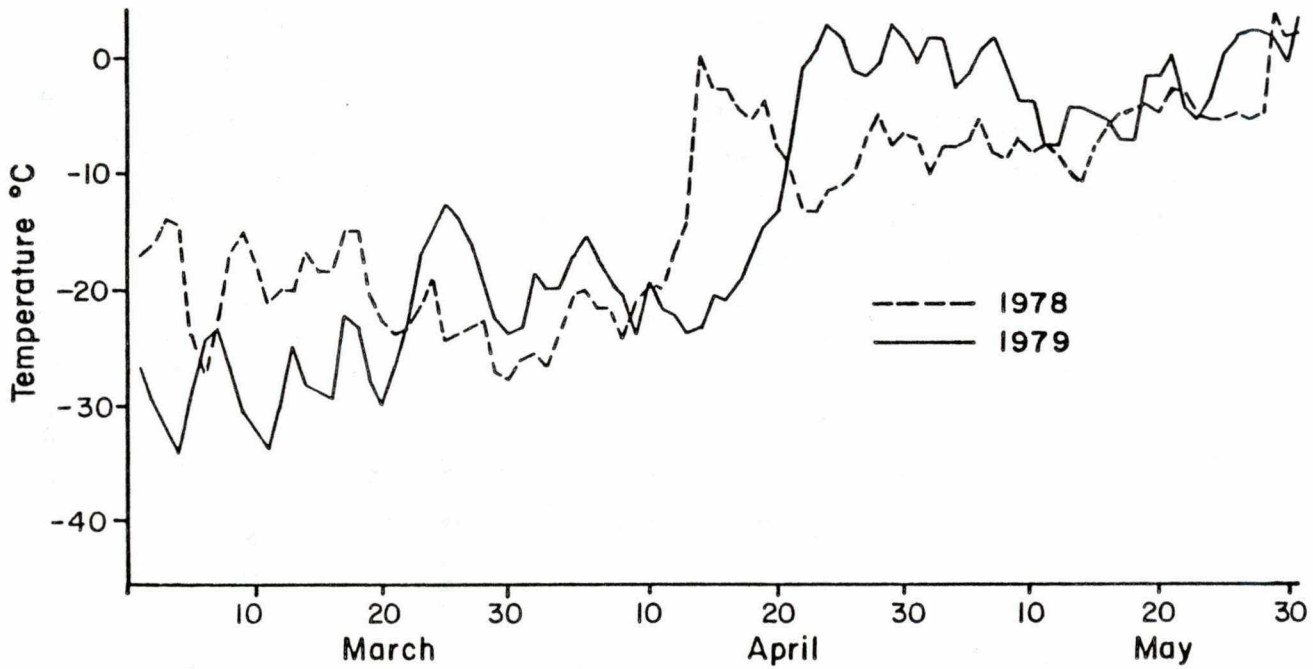

Figure 10. Daily maximum temperatures at Barter Island, Alaska for March, April and May in 1978 and 1979 (from National Weather Service 1978, 1979).

speculated that each spring a 10- to 14-d period of warm weather apparently cued the highly variable onset of reproduction in L. sibericus. The spring warm period in 1979 may have triggered breeding, the subsequent loss of snow cover and lack of green forage might then have caused high mortality of reproductive animals and low recruitment of juveniles. No explanation can be found in the weather data for the continued failure in productivity after green-up at its usual time in June. Mortality remained high in all weight classes and recruitment low throughout summer.

Populations of D. torquatus were low both years and weight distributions were quite similar. However, the low number of captures makes analysis questionable. M. oeconomus populations increased through both summers with nearly identical weight distributions typical of a seasonal cycle of abundance.

D. Habitat use

Capture locations of microtines overlapped somewhat, but occurred on a general gradient of moisture with most D. torquatus captures in drier uplands, most L. sibericus captures in mesic medium relief polygonized terrain, and most M. oeconomus captures in the lush, wet Dupontia meadow (Table 9). All 3 species are known to exhibit seasonal changes in habitat use similar to that found in this study. Although the winter and/or breakup habitats of M. oeconomus were not located, the dozer trail appeared to provide refuge habitat for both lemming species during breakup. After breakup, all but a few

Table 9. Vegetation types of small mammal capture locations at Demarcation Bay, Alaska. Codes are as defined in Table 1. Data from 1978 and 1979 are combined.

Vegetation Type	*Lemmus sibericus*				*Dicrostonyx torquatus*				*Microtus oeconomus*			
	period 1	per 2	per 3	total	per 1	per 2	per 3	total	per 1	per 2	per 3	total
CM	0	1	2	3	0	0	0	0	0	0	0	0
DM	4	9	1	14	0	0	0	0	2	7	15	24
DCM	0	2	3	5	0	0	0	0	0	0	0	0
FB	0	0	1	1	1	2	2	5	0	0	0	0
LR	1	0	4	5	0	0	0	0	0	0	0	0
MR	10	7	2	19	5	2	0	7	0	3	3	6
TS	1	0	3	4	0	0	0	0	0	0	0	0
TER	1	0	2	3	0	0	0	0	0	0	0	0
HCP	1	3	4	8	4	3	0	7	0	0	0	0
CP	0	0	0	0	0	0	0	0	1	1	2	4
DT	35	13	17	65	2	0	0	2	0	0	0	0
ST	2	4	8	14	5	0	1	6	0	0	0	0

reproductive L. sibericus dispersed to various other vegetation/landform types. Similar seasonal changes in habitat of L. sibericus have been documented by Krebs (1964) and Batzli et al. (1980).

As shown in Table 9, captures of L. sibericus occurred in a number of vegetation types. By far the greatest number of captures occurred in the dozer trail (46%). Medium relief lcp were second in importance with 13.5% of captures. Small numbers of captures occurred in every vegetation type sampled with the exception of high relief lcp and coastal ponds, though single captures in some areas may have been transients rather than residents.

Table 10 presents a vegetative description of actual capture sites. The occurrence of so many L. sibericus captures in disturbed vegetation types (i.e. the dozer trail) affects the interpretation of capture site descriptions. The trap sites in disturbed vegetation types had much greater microrelief than those in undisturbed sites. Salix spp. were uncommon in trap sites in disturbed vegetation types and seemed to be replaced by herbaceous species and Luzula spp. In general, the dozer trail provided juxtaposition of lush, wet foraging areas with dry burrows and runway systems in the easily excavated peat mounds, which was an exaggeration of the vegetation and relief patterns characteristic of the undisturbed trap sites of L. sibericus. Measures of three physical parameters are indicative of sites with a juxtaposition of dry and wet microhabitats: average microrelief (21.2 cm, SD=13.21), average number of vascular plant species (11.7,

Table 10. Vegetative descriptions of small mammal capture sites at Demarcation Bay, Alaska. Standard deviation for each parameter given in parentheses where appropriate.

	Lemmus sibericus	*Dicrostonyx torquatus*	*Microtus oeconomus*
Number of samples	141	27	34
Physical parameters			
Average microrelief (cm)	21.2 (13.2)	18.3 (9.5)	13.3 (6.4)
Average number of species	11.7 (4.4)	13.7 (3.4)	9.2 (3.6)
Average height of vegetation (cm)	8.5 (5.0)	8.6 (4.8)	11.1 (5.2)
Average moisture index	2.6 (1.4)	2.2 (1.0)	3.6 (1.0)
Percent cover values			
Carex aquatilis	29.9 (32.8)	26.2 (33.7)	5.9 (20.4)
Carex bigelowii	3.2 (10.9)	10.9 (16.3)	0.0 -
Other rhizomatous Cyperaceae	2.9 (13.7)	3.3 (12.7)	0.6 (3.4)
Eriophorum angustifolium	2.2 (8.1)	0.0 -	3.5 (6.1)
Dupontia fischeri	9.6 (26.9)	5.7 (14.0)	63.6 (35.6)
Other rhizomatous Graminae	1.7 (6.5)	0.4 (1.9)	1.6 (5.5)
Moss	12.8 (17.2)	8.5 (9.5)	0.6 (2.4)
Lichen	2.4 (5.9)	4.7 (9.1)	0.0 -
Salix reticulata	2.6 (5.2)	6.2 (6.6)	0.0 -
Salix arctica	5.5 (8.4)	7.1 (7.9)	0.0 -
Salix phlebophylla	0.4 (2.7)	2.3 (5.4)	0.0 -
Poa spp.	4.1 (13.1)	3.3 (5.6)	3.8 (7.3)
Eriophorum vaginatum	1.6 (6.2)	6.3 (10.7)	0.0 -
Bare ground	12.0 (20.4)	5.4 (12.1)	3.7 (17.3)
Water	1.0 (6.4)	1.1 (4.9)	2.7 (13.0)
Tufted Cyperaceae	0.5 (2.3)	0.0 -	0.0 -
Tufted Graminae	0.6 (2.5)	1.6 (4.1)	2.2 (5.4)
Heath	0.9 (5.2)	3.0 (6.1)	0.0 -
Percent cover values (continued)			
Luzula spp.	1.5 (4.8)	0.4 (1.9)	0.0 -
Saxifragaceae	1.2 (3.3)	0.4 (1.6)	2.6 (4.8)
Caryophyllaceae	2.1 (6.1)	0.3 (1.1)	0.0 -
Other	0.8 (2.2)	1.4 (5.1)	8.8 (28.8)
Total rhizomatous Cyperaceae	38.2 (33.9)	40.4 (30.0)	10.0 (20.4)
Total Graminae	16.0 (29.2)	10.9 (15.6)	80.1 (27.5)
Total *Salix*	8.5 (12.4)	15.7 (13.9)	0.0 -
Total herbaceous	4.9 (10.0)	4.0 (6.1)	2.6 (4.8)
Total graminoid	57.8 (33.3)	58.0 (25.0)	90.1 (21.6)
Total woody	8.5 (12.4)	15.7 (13.9)	0.0 -
Average number of species in group			
Legumes	0.0 (0.2)	0.1 (0.4)	0.0 -
Salix	1.2 (0.8)	2.0 (0.9)	0.3 (0.5)
Herbaceous	5.4 (2.5)	6.2 (2.1)	4.8 (2.1)
Graminoid	3.2 (1.6)	3.1 (1.2)	3.0 (1.2)
Heath	0.2 (0.4)	0.7 (0.7)	0.0 -
Woody	1.2 (0.9)	2.2 (1.0)	0.3 (0.5)
Percent of plots with group present			
Legumes	2.1	14.8	0.0
Salix	79.4	92.6	35.3
Herbaceous	93.6	100.0	97.1
Graminoid	99.3	100.0	100.0
Heath	17.7	59.3	0.0
Woody	79.4	92.6	35.3
Total number of species at all capture sites	60	46	30

SD=4.37) and average moisture index (2.6, SD=1.42). Average microrelief is high, which indicates sites located on the slope between a trough or polygon center and a ridge. The number of plant species per m^2 is also high and shows great variability, indicating that capture sites included dry microsites which have high diversity. Similarly, the moisture index shows high variability. Further indicators that captures occurred on sites with a mosaic of wet and dry microhabitats are that plant species common to both extremes of moisture show relatively high frequency of occurrence and that no particular plant species appears to characterize L. sibericus capture locations. The most frequent plant species (from most to least frequent) were C. aquatilis, P. viviparum, S. arctica, S. cernua, Saxifraga hirculus, and S. longipes, all of which are widespread in moist tundra.

D. torquatus captures occurred in medium relief lcp, high center polygons, sled tracks, frost boils and, in early summer, on the dozer trail (Table 10). No captures were made in wet vegetation types. Capture sites had many distinctive characteristics (Table 10), including high average microrelief (46.5 cm) and low average moisture index (2.2) indicating a large proportion of dry sites. The average number of plant species per m^2 trap site (13.7) seems low for dry sites, but is probably due to the small sample size. The average is, nonetheless, larger than that for capture locations of the other 2 microtines. C. bigelowii, lichen, S.. reticulata, S. phlebophylla, E. vaginatum and heath cover values were all higher at D. torquatus

capture sites than at those of other microtines. Total woody vegetation averaged 15.7% cover and 2.2 woody species per plot. The average number of herbaceous species per plot was also high at 6.2, and 100% of plots had herbs present. Legumes and heath associates also had high frequency of occurrence. The most common plant species present at D. torquatus capture sites were (in order of frequency): S. arctica, P. viviparum, S. reticulata, and S. longipes. Characteristic species (i.e. species having higher frequency at trap sites than in the vegetation type at large) are numerous, including C. bigelowii (44% occurrence), D. integrifolia (44%), E. vaginatum (33%), P. capitata (26%), S. phlebophylla (30%), V. vitis-idaea (22%), and S. atropurpureus (30%). The habitat preferences of D. torquatus are well-defined but the dry microsites with increased presence and cover of woody and herbaceous dicots occur in a number of vegetation types through which the animals appear to be dispersed (Table 9).

M. oeconomus captures were limited to Dupontia meadow (70.6%) and the adjacent medium relief lcp and coastal ponds (Table 9). Capture locations were characterized by low relief (34 cm ave), low diversity (9.2 species per m^2), lush vegetation (29 cm ave height), and a high moisture index (3.58). C. aquatilis had a very low cover value of 5.9%, being displaced by D. fischeri (63.6% cover). Graminoid vegetation (90.1% cover) was much more prominent at M. oeconomus capture sites than it was at capture sites of either lemming. All capture sites had less than 1% woody cover. Characteristic plant species at M. oeconomus capture locations included C. tetrandum (73%

occurrence), D. fischeri (91%), E. angustifolium (71%), E. schuechzeri (6%), M. apetalum (62%), and S. cernua (82%). M. oeconomus showed the most restricted habitat preferences and did not expand to other areas as numbers increased. M. oeconomus is a habitat specialist, and at low densities appeared to be able to exclude L. sibericus from Dupontia meadow habitats (see also Rausch and Rausch 1975).

AVIAN INVESTIGATION

I. RESULTS AND DISCUSSION

Scientific and common names of all bird species encountered appear in Appendix 5. In 1978, 43 nests of 7 species were monitored: 14 Lapland longspur; 12 semipalmated sandpiper; 10 pectoral sandpiper; 4 red-necked phalarope; 1 red-throated loon; 1 red phalarope; and 1 buff-breasted sandpiper. Of these nests, 2 longspur and 4 semipalmated sandpiper nests were located just outside the 30-ha plot; the defended territories associated with these nests included portions of the plot.

In 1979, 48 nests of 12 species were monitored: 22 Lapland longspur; 12 semipalmated sandpiper; 3 red-necked phalarope; 2 pectoral sandpiper; 2 Baird's sandpiper; 1 red phalarope; 1 willow ptarmigan; 1 green-winged teal; 1 red-throated loon; 1 sandhill crane; 1 lesser golden-plover; and 1 oldsquaw. Forty-one nests were on the 30-ha study plot: 21 longspur, 10 semipalmated sandpiper, 2 pectoral sandpiper, 3 red-necked phalarope, 1 red phalarope, 1 willow ptarmigan, 1 green-winged teal, 1 Baird's sandpiper and 1 red-throated loon.

There were 2 notable changes in abundance between 1978 and 1979: an increase in numbers of Lapland longspurs and a decrease in numbers of pectoral sandpipers. Both species are noted for local fluctuations in nest densities. The increased numbers of longspurs may have been due in part to earlier availability of snow-free nesting habitat in 1979 (Fig. 10).

A. Phenology

Lapland longspur

Sufficient data were available to examine the phenology of 13 and 18 longspur nests in 1978 and 1979, respectively. The years were markedly different. In 1978, the average date of nest initiation was 19 June (Fig. 11). This is much later than the average date of 3 June in 1979, exclusive of probable renest attempts. Although data on nest locations in 1978 identify only one probable renest attempt, several of the late nests were undoubtedly second nests. The 1978 nesting season was interrupted by a snowstorm from 21 to 24 June, which caused 3 of 7 known nests to be abandoned. Six of 13 nests for which phenology data were computable were begun 2 to 5 d after the storm subsided on 24 June. None of these was less than 110 m from a known abandoned nest and none were considered renest attempts by birds from a previously located nest. However, the storm and consequent nest failures occurred early in the 1978 season and it is possible that a portion of these post-storm nests were replacements of previously unlocated nests. A reduction in the average clutch size of longspurs from 5.4 prior to 21 June to 4.7 after 21 June supports the contention that at least some of the late nests were renest attempts (Table 11). On the other hand, even when nests initiated later than 21 June are excluded from the calculation, the average date of nest initiation in 1978 was 12 June, considerably later than the 1979 date.

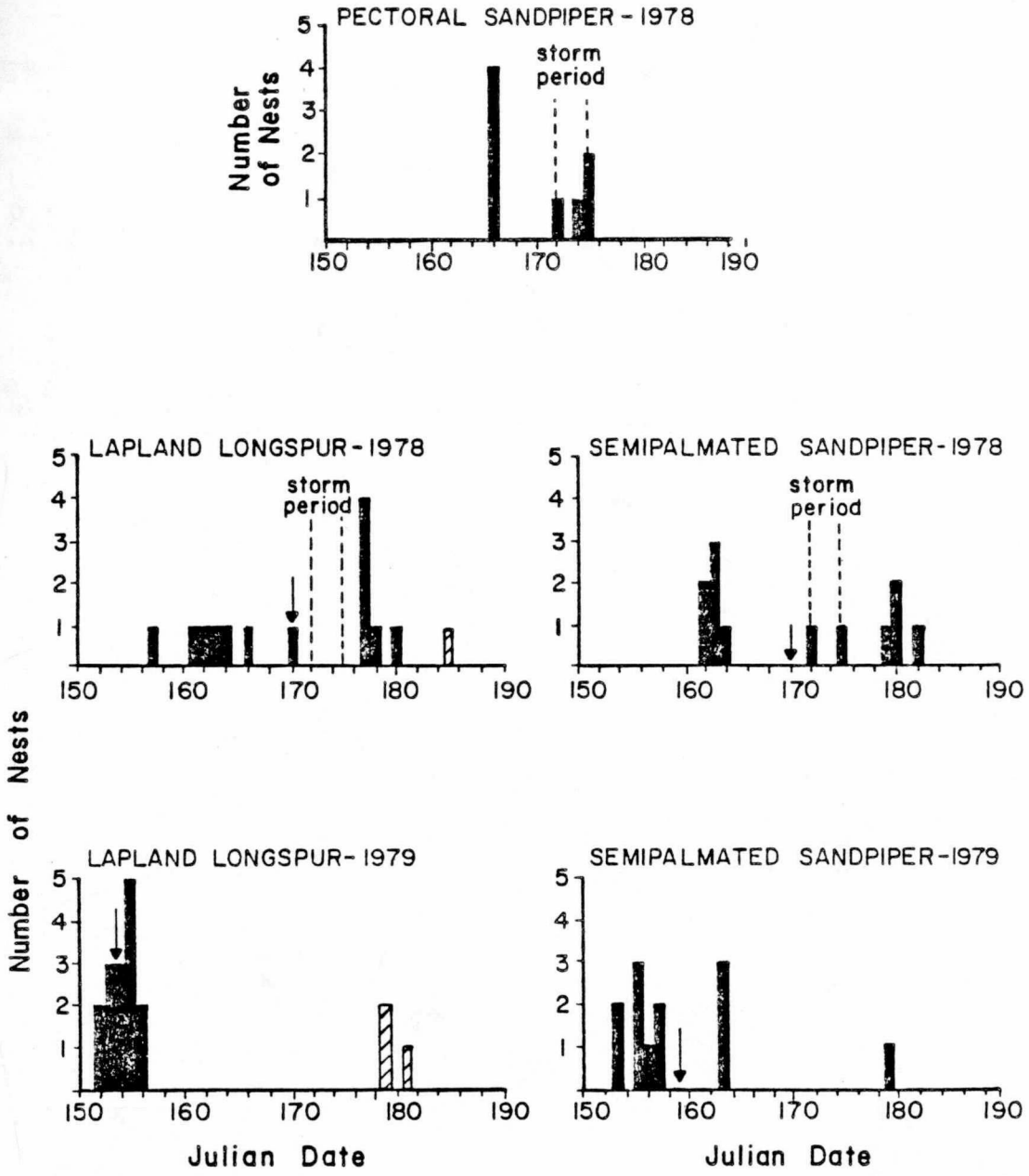

Figure 11. Dates of initiation of bird nests at Demarcation Bay, Alaska in 1978 and 1979. Arrows indicate mean date of nest initiation.

Table 11. Average clutch sizes of the 4 most common breeding species at Demarcation Bay, Alaska. Number of nests given in parentheses.

Date of initiation	Lapland Longspur		Semipalmated Sandpiper		Pectoral Sandpiper		Red-necked Phalarope	
1978								
prior to 21 June	5.4	(7)	4.0	(6)	4.0	(4)	4.0	(2)
after 21 June	4.4	(7)	3.5	(6)	4.0	(4)	4.0	(2)
average	4.9	(14)	3.7	(12)	4.0	(10)	4.0	(4)
1979								
prior to 21 June	5.3	(15)	4.0*	(11)	4.0	(1)	3.7	(3)
after 21 June	3.6	(7)	4.0	(1)	4.0	(1)	-	(-)
average	4.8	(22)	4.0	(12)	4.0	(2)	3.7	(3)

Semipalmated sandpiper

The average date of initiation of 12 semipalmated sandpiper nests in 1978 was 19 June. Fig. 11 shows a clearly bimodal distribution of initiation dates. Although this would lead one to suspect that at least some of the nests initiated after 21 June were renest attempts, the nest records indicate that none could be related to a known failed nest. Semipalmated sandpiper nests are much easier to find during the last half of incubation and it is highly likely that at least some late nests represent renest attempts of pairs with a previously unlocated, failed nest. Similar to longspurs, the average clutch size was lower subsequent to the 21 June storm: 4.0 prior to 21 June and 3.5 after (Table 11). However, sandpipers are determinate layers and some of the 3-egg clutches observed may have resulted from the loss of an egg due to lack of snow-free nest sites, rather than indicating a second nesting attempt.

In contrast to 1978, nesting of semipalmated sandpipers was highly synchronous in 1979 and the average date of nest initiation was 8 June.

Other species were not numerous enough for individual analysis of nest initiation. The average date for initiation of 8 pectoral sandpiper nests in 1978 was also 19 June (Fig. 11). In 1979 only 2 pectoral sandpiper nests were found.

General discussion

Nest initiation of all species was dramatically different in the 2 years. Nesting was initiated late in 1978 and was interrupted by a

snowstorm which covered available nest sites for 5 to 8 d. Some nests were abandoned as a result, but some birds were observed incubating beneath the snow, having established a small tunnel for access to the nest site. Nest initiation was, therefore, clearly bimodal in 1978, due to either renesting attempts (which could not be documented) or to a delay in establishment of a nest site until the laying of the second egg.

A general summary of nesting is provided in Fig. 12. All species are lumped here as an indication of the general availability of active nests to foxes. The contrast in synchrony between the 2 years and the effects of the June storm are clearly evident. The 1978 season began with a degree of synchrony and appeared to reach a plateau between 15 and 20 June. Abandonment during the storm reduced the number of active nests prior to a resurgence of breeding activity which brought the total number of active nests to a peak of 30 on 1 July. After 1 July, fledging and 5 asynchronous nest failures account for the gradual attrition in active nests through 25 July.

The 1979 season showed a high degree of synchrony and breeding was undisturbed until shortly after longspurs began to hatch between 19 and 25 June. A sharp decline in the number of active nests occurred at that time, due in part to predation on longspurs, which was concentrated during the hatching period, and in part to the successful fledging of most sandpiper nests between 23 and 29 June. A small number of very late nest attempts, mostly by longspurs, extended the nesting season through 29 July.

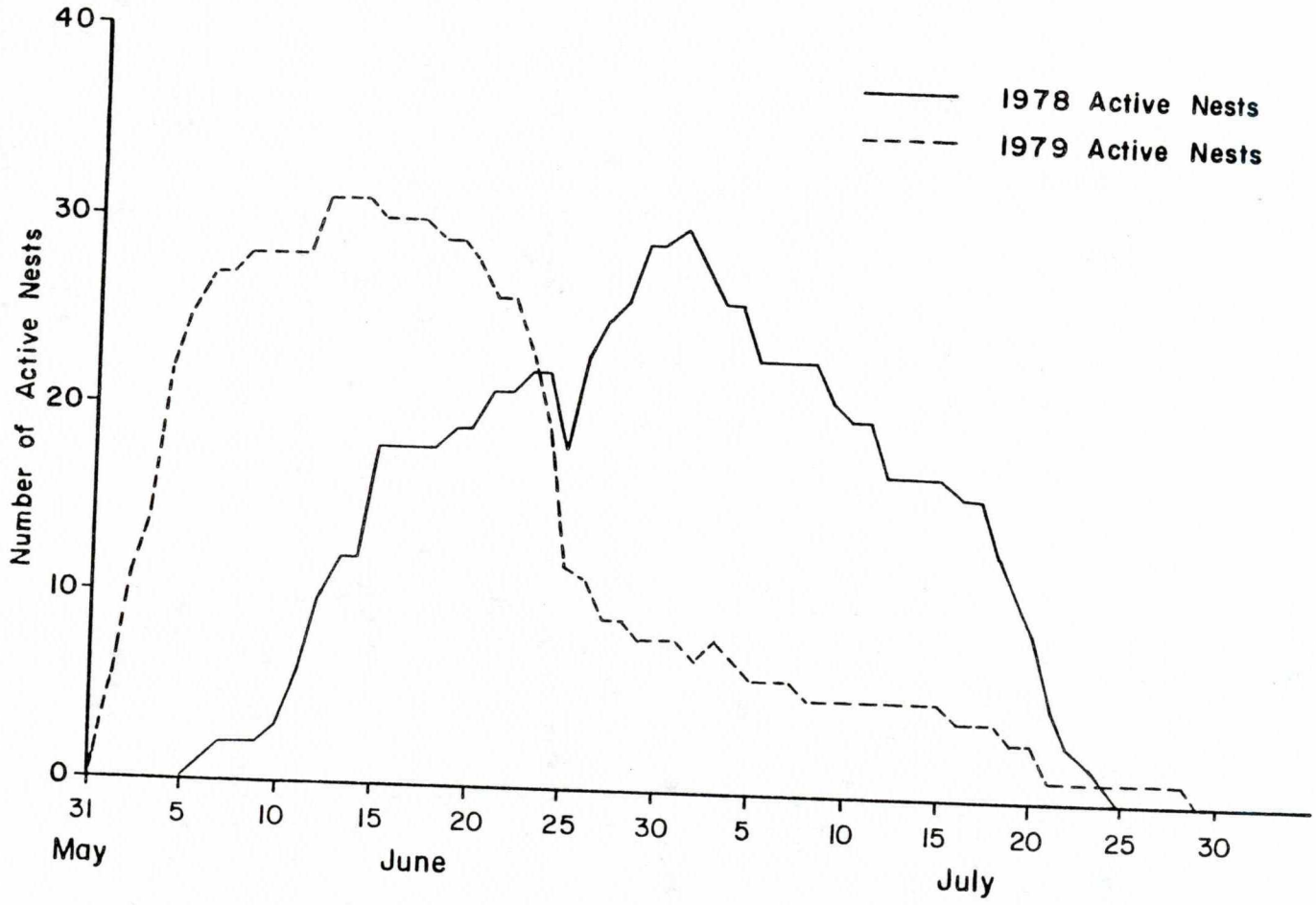

Figure 12. Number of bird nests active each day in 1978 and 1979 at Demarcation Bay, Alaska.

B. Nest losses and productivity

Clutch sizes are shown in Table 11 and nest losses are summarized in Table 12. A nest was considered successful if at least one chick was fledged. All nest failures were attributable to one of 3 factors: predation, unfavorable weather or trampling by caribou. Nest success was 60.5% in 1978. The June storm had a definite effect on nest success; 42.1% of nests initiated before 19 June were successful, as opposed to 78.9% after 19 June. Of the 17 failures, 10 were attributable directly to weather. Eight of these were abandoned on 21 June; eggs in the remaining 2 were incubated after 21 June but failed to hatch. Predation was unimportant, affecting 5 nests, and could not be definitely attributed to any single predator, although it was suspected that jaegers were responsible. In addition, 2 clutches were trampled by caribou, as were some individual eggs and chicks from otherwise successful nests. The occurrence of a snowstorm at the peak of incubation was the most significant factor affecting nest success.

Contrary to the results from 1978, predation was the primary cause of nest failure in 1979. Only 39.6% of the nests were successful. Of the 29 nests which failed, 27 were lost to foxes. Predation was unevenly distributed among species; longspurs suffered 95.4% nest failure due to predation as opposed to 8.3% for semipalmated sandpipers. Other species effected were green-winged teal (1 nest failed/1 nest observed), Baird's sandpiper (1/2), red-throated loon (1/1), oldsquaw (1/1), and willow ptarmigan (1/1). All of these losses were attributed to predation by arctic foxes. One

Table 12. Factors responsible for losses of nests and chicks/eggs at Demarcation Bay, Alaska in 1978 and 1979. Nests are considered successful if at least one chick is fledged. Totals include nests both on and off the 30-ha study plot.

	All Species	Lapland Longspur	Semipalmated Sandpiper	Pectoral Sandpiper	Red-necked Phalarope
1978					
Total nests	43	14	12	11	4
Total nests lost to:					
1) predation	5[1]	1	0	2	1
2) weather	10[2]	3	2	3	1
3) caribou	2	1	0	1	0
Total nest loss	17	5	2	6	2
Proportion of total	0.39	0.36	0.17	0.54	0.50
Total chicks/eggs	183	69	45	44	16
Loss to: 1) predation	22	3	0	8	4
2) weather	42-57	17-28	8-10	12-15	4
3) caribou	10	3	1	4	0
Total chicks/eggs lost	89	23-24	9-11	24-27	8
Proportion of total	0.48	0.33-0.49	0.20-0.24	0.54-0.61	0.50
1979					
Total nests	48	22	12	2	3
Total nests lost to:					
1) predation	27[3]	21	1	0	0
2) weather	(2)[4]	1	0	0	0
Total nest loss	29	22	1	0	0
Proportion of total	0.60	1.00	0.08	0.00	0.00
Total chicks/eggs	204	105	48	8	11
Loss to: 1) predation	126	103	4	0	0
2) weather	4	2	0	0	0
Total chick/egg loss	130	105	4	0	0
Proportion of total	0.64	1.00	0.08	0.00	0.00

[1] Includes 1 red phalarope nest.

[2] Includes a red-throated loon nest with 1 egg which was flooded after the 21 June storm. The same or another egg was found on a poorly constructed nest platform approximately 10 m from the first. This egg was crushed by caribou on 30 June. Another egg was laid on the former nest platform but was finally abandoned, presumably due to daily activities on the study plot.

[3] Includes 1 Baird's sandpiper, 1 willow ptarmigan, 1 green-winged teal, 1 red-throated loon and 1 oldsquaw.

[4] Includes 1 sandhill crane nest in which neither egg hatched and was finally abandoned.

failure of longspur and one of sandhill crane were attributed to weather in 1979 because the eggs failed to hatch. However, no particular weather event could be identified as the prime cause of these failures. The Porcupine caribou herd migration for the most part missed the study plot in 1979 and no losses were attributed to trampling by caribou.

The dramatic difference between years in nests lost to fox predation was apparently due to the extremely low availability of alternate prey in 1979. Brown and collared lemmings are preferred prey of arctic foxes on the north slope and reproduction of foxes has been shown to be closely related to their availability (Speller 1972). In 1978, a pair of foxes successfully reared 9 pups at a den within 0.5 km of the study plot without seriously affecting avian production on the plot. Observations indicated that small mammals were the primary food of the pups. Foxes did not breed in the Demarcation Bay area in 1979 and the adults fed primarily on eggs in mid-summer.

Although our study may have had an effect on the rate of predation, the impact should have been less in 1979 due to greater care taken in nest marking and checking as fox predation increased in frequency. The 1978 nests were at least as susceptible as the 1979 nests, with the food requirements of the foxes greater in 1978 due to pup production. The greater loss in 1979 to fox predation is attributable to a change in the behavior and food habits of foxes in response to decreased availability of preferred small mammal prey. However, this does not exclude the possibility of behavioral

alterations in the response of foxes to the study plot. Any increased activity of arctic foxes on the study plot which may have occurred in 1979 would produce a low estimate of avian productivity for the Demarcation Bay area.

The results of the nesting study indicate that longspur nests are more susceptible to predation by foxes than are sandpiper nests. For 18 longspur nests the exact stage at failure was known; of these 18, 16 failed during the nestling stage. This is surely the most vulnerable period to predators that use sound and smell to locate prey. Sandpipers have no nestling stage. Although limited, the data also show a greater rate of failure caused by weather for pectoral sandpipers and red-necked phalaropes than for semipalmated sandpipers. This increased rate may be due to non-continuous incubation (by the female alone in pectoral sandpipers and by the male alone in red-necked phalaropes) contributing to egg chilling. Semipalmated sandpipers appeared somewhat less susceptible than other species to loss due to predation in 1978. This may have been because the continuous incubation by both male and female semipalmated sandpipers makes the eggs less conspicuous to avian predators, which were believed to be the major egg predators in 1978.

More accurate estimates of productivity are possible by treating eggs (or chicks) separately. Table 13 presents productivity estimates. In 1978, many eggs even in successful clutches failed to develop and several individual chicks were found dead after caribou herds entered the study plot. Both nest and egg/chick analyses show

Table 13. Avian productivity on the 30-ha study plot at Demarcation Bay, Alaska.

	All Species	Lapland Longspur	Semipalmated Sandpiper	Pectoral Sandpiper	Red-necked Phalarope
1978					
Number of nests on plot	37	12	8	10	4
Egg production on plot	153	59	29	40	16
Egg/chick loss to:					
1) predation	13[1]	0	8	4	
2) weather	38-53	7-24	4-6	12-15	4
3) caribou	10	3	1	4	0
Number fledged	72	29	22	16	8
Fledged per nest	1.9	2.4	2.7	1.3	2.0
1979					
Nests on plot	41	21	10	2	3
Egg production on plot	176	101	40	8	11
Egg/chick loss to:					
1) predation	112	99	4	0	0
2) weather	2	2	0	0	0
Number fledged	62	0	36	8	11
Fledged per nest	1.5	0.0	3.6	4.0	3.7

[1] Includes 1 red phalarope nest.

clearly that, through repeat nest attempts, longspur reproductive effort was higher in 1979 with virtually no success. Reproductive effort of semipalmated sandpipers was similar in both years and, although loss to predation was higher in 1979, overall productivity was improved due to more favorable climatic conditions. Pectoral sandpiper reproductive effort decreased from 1978 to 1979 while red-necked phalarope reproductive effort remained relatively constant. Overall productivity of shorebirds was higher in 1979 than in 1978 in spite of high levels of fox predation and lower shorebird nest density.

In summary, 2 factors accounted for the variation in nest success and net productivity between years: 1) snow during incubation in 1978, and 2) intense predation, particularly on longspurs, by foxes in 1979. The effects of caribou are likely to be small and localized although in some restricted areas they may be more severe than even the 1978 results indicated. Many localized areas outside the study plot, through which large numbers of caribou were funneled (due to lakes and other geographic features) were very disturbed with probable elimination of successful nesting. However, the area-wide impacts are likely to be small.

C. Habitat use

Preference ratios for each species in each vegetation type were calculated by dividing the observed number of nests in that vegetation

type on the 30-ha plot by the expected value assuming no preferences. Expected values for each vegetation type were calculated by multiplying the total number of nests of each species on the plot by the proportion of the study plot covered by that type. Expected values are too low for a statistical analysis; however, ratios for all but the rare vegetation types provide a good indication of relative vegetation type preferences.

Lapland longspur

Lapland longspurs were the most abundant breeders and had the most catholic vegetation type preferences. Nests were found in every vegetation type except wet Carex and Dupontia meadows, Arctophila marsh, and coastal ponds (Table 14). The preference ratios in Table 15 indicate distinct vegetation type preferences. The wettest vegetation types appeared to be avoided, as were frost-boil tundra and coastal ponds, which have low microrelief and low vegetation height. Nests were more frequent than expected in the 3 most common vegetation types on the 30-ha study plot, dry Carex meadow, low relief lcp, and high center polygons. Although the low expected values inflate the preference ratios, high relief lcp and tussock slope appeared to be highly preferred.

Nest site characteristics are summarized in Table 15. The data are from 1-m^2 plots and describe microhabitats within each vegetation type which are characteristic of the nest site. Longspur nest sites were characterized by higher relief than those of other bird species, averaging 41 cm. Their nests were typically sheltered

Table 14. Vegetation type preferences of nesting birds on the 30-ha study plot at Demarcation Bay, Alaska in 1978 and 1979. Observed values (obs) are the actual number of nests in each vegetation type. Expected values (exp) for each vegetation type are calculated by multiplying the total number of nests of each species by the proportion of the study plot covered by that type. Codes are as defined in Table 1.

Vegetation type (proportions of study plot)	Lapland Longspur			Semipalmated Sandpiper			Pectoral Sandpiper			Red-necked Phalarope			All species combined		
	obs	exp	ratio	obs	exp	ratio	obs	exp	ratio	obs	exp	ratio	obs	exp	ratio
CM (0.06)	0	1.92	0	1	1.20	0.83	0	0.72	0	1	0.42	2.38	3	4.62	0.65
DM (0.02)	0	0.64	0	0	0.40	0	0	0.24	0	0	0.14	0	0	1.54	0
DCM (0.13)	5	4.16	1.20	3	2.60	1.15	3	1.56	1.92	3	0.91	3.30	14	10.01	1.40
LR (0.17)	7	5.44	1.29	6	3.40	1.76	1	2.04	0.49	1	1.19	0.84	17	13.09	1.30
MR (0.08)	1	2.56	0.39	3	1.60	1.87	2	0.96	2.08	0	0.56	0	5	6.16	0.81
HR (0.01)	2	0.32	6.25*	1	0.20	5.00*	0	0.12	0	0	0.07	0	3	0.77	3.90*
TS (0.06)	4	1.92	2.08	0	1.20	0	0	0.72	0	0	0.42	0	4	4.62	0.86
HCP (0.17)	7	5.44	1.29	0	3.40	0	0	2.04	0	1	1.19	0.84	10	13.09	0.76
AM (0.02)	0	0.64	0	0	0.40	0	0	0.24	0	0	0.14	0	1	1.54	0.65
TER (0.09)	3	2.88	1.04	4	1.80	2.22	2	1.08	1.85	0	0.63	0	9	6.93	1.30
FB (0.08)	2	2.56	0.78	2	1.60	1.25	1	0.96	1.04	0	0.56	0	5	6.16	0.81
DT (0.05)	0	1.60	0	0	1.00	0	1	0.60	1.67	1	0.35	2.85	3	3.85	0.78
ST (0.02)	1	0.64	1.56	0	0.40	0	2	0.24	8.33	0	0.14	0	3	1.54	1.95
CP (0.01)	0	0.32	0	0	0.20	0	0	0.12	0	0	0.07	0	0	0.77	0
	32			20			12			7			77		

* These preference ratios are overestimates due to the very low expected values. This habitat was sampled insufficiently for an assessment of use.

Table 15. Vegetative descriptions of bird nest locations at Demarcation Bay, Alaska in 1978 and 1979. Standard deviation for each parameter given in parentheses where appropriate.

	Lapland longspur	Semipal sandpiper	Pectoral sandpiper	Red-necked phalarope
Number of samples	35	21	11	6
Physical parameters				
Average microrelief (cm)	16.0 (5.4)	10.3 (2.2)	10.5 (2.1)	10.7 (2.3)
Average number of species	12.4 (3.6)	11.3 (2.3)	10.1 (2.0)	8.0 (2.8)
Average height of vegetation (cm)	9.2 (3.2)	9.4 (3.6)	8.0 (2.8)	14.0 (5.3)
Average moisture index	1.7 (0.8)	1.9 (1.1)	2.1 (1.4)	3.3 (1.9)
Percent cover values				
Carex aquatilis	39.4 (32.9)	54.1 (29.7)	63.6 (30.3)	64.2 (24.0)
Carex bigelowii	13.8 (23.6)	5.0 (20.7)	5.9 (19.6)	0.0 -
Other rhizomatous Cyperaceae	2.1 (12.7)	9.5 (15.6)	2.3 (7.5)	0.0 -
Eriophorum angustifolium	0.0 -	0.0 -	0.9 (3.0)	5.0 (12.2)
Dupontia fischeri	0.9 (5.1)	6.7 (19.0)	0.0 -	0.0 -
Other rhizomatous Graminae	2.9 (12.7)	0.0 -	3.6 (12.1)	4.2 (10.2)
Moss	5.4 (6.3)	1.7 (3.6)	1.4 (3.2)	3.3 (6.0)
Lichen	1.9 (4.2)	0.0 -	0.0 -	2.5 (6.1)
Salix reticulata	8.3 (7.5)	10.3 (8.8)	9.5 (10.6)	1.7 (4.1)
Salix arctica	12.5 (14.5)	5.5 (9.6)	6.4 (7.8)	8.3 (12.1)
Salix phlebophylla	0.8 (2.5)	0.2 (1.1)	0.0 -	0.0 -
Poa sp.	0.6 (1.6)	0.0 -	0.00 -	0.0 -
Eriophorum vaginatum	5.3 (11.1)	0.0 -	0.4 (1.5)	0.0 -
Bare ground	0.2 (1.0)	0.0 -	0.4 (1.5)	1.2 (2.0)
Water	0.0 -	0.0 -	0.0 -	0.0 -
Tufted Cyperaceae	1.1 (6.8)	1.4 (6.5)	2.7 (9.0)	8.8 (13.9)
Tufted Graminae	0.1 (0.8)	0.0 -	0.0 -	0.0 -
Heath	3.8 (7.2)	4.6 (8.6)	2.7 (4.7)	0.0 -
Percent cover values (continued)				
Luzula spp.	0.3 (1.2)	0.0 -	0.0 -	0.0 -
Saxifragaceae	0.2 (0.9)	0.2 (1.1)	0.0 -	0.0 -
Caryophyllaceae	0.0 (0.2)	0.0 -	0.0 -	0.0 -
Other	0.2 (1.2)	0.7 (3.3)	0.0 -	0.0 -
Total rhizomatous Cyperaceae	53.8 (26.7)	68.6 25.3)	72.7 (16.6)	69.2 (19.3)
Total Graminae	4.3 (13.3)	7.4 (21.1)	3.6 (12.1)	4.2 (10.2)
Total *Salix*	21.2 (13.7)	16.0 (12.7)	15.9 (14.8)	10.0 (13.8)
Total herbaceous	3.9 (7.3)	4.9 (8.5)	2.7 (4.7)	0.0 -
Total graminoid	64.7 (18.6)	77.4 (16.0)	79.5 (13.5)	82.2 (23.3)
Total woody	21.1 (13.9)	16.3 (12.9)	15.9 (14.8)	10.0 (13.8)
Average number of species in group				
Legumes	0.3 (0.2)	0.0 -	0.0 -	0.0 -
Salix	2.2 (0.6)	2.0 (0.3)	1.8 (0.4)	1.3 (0.8)
Herbaceous	4.7 (2.5)	4.4 (1.6)	4.3 (1.9)	2.8 (1.7)
Graminoid	2.6 (1.2)	2.3 (1.2)	1.8 (1.1)	2.3 (0.8)
Heath	1.0 (0.8)	1.0 (0.5)	0.8 (0.6)	0.2 (0.4)
Woody	2.3 (0.8)	2.0 (0.5)	1.9 (0.5)	1.3 (0.8)
Percent of plots with group present				
Legumes	2.9	0.0	0.0	0.0
Salix	100.0	100.0	100.0	83.3
Herbaceous	100.0	100.0	100.0	83.3
Graminoid	100.0	100.0	100.0	100.0
Heath	74.3	85.7	72.7	16.7
Woody	100.0	100.0	100.0	83.3
Total number of species at all nest sites	43	37	25	15

under overhanging tussocks or willows and required some microrelief. Longspur nest sites were also characterized by drier locations (moisture index average 1.7) with a higher plant diversity (12.3 species per m^2) than were nest sites of the common sandpipers. E. vaginatum and S. arctica, two species which formed an integral part of many longspur nests, averaged 5.3% cover and 12.5% cover, respectively, and occurred with a frequency of 28.6% and 94.3%, respectively. Total woody vegetation averaged 21.1% cover, a higher value than that attained at nest sites of other species. Total graminoid cover at longspur nest sites of 64.7% was lower than at nest sites of other species. Cover values and frequency of other plant species are indicative of the variability in habitats used. The common species are typical of drier microhabitats: C. bigelowii, cover 13.8%, frequency 34.3%; D. integrifolia, 71.4% occurrence; S. phlebophylla, 22.9% occurrence; S. reticulata, 94.3% occurrence; and S. longipes, 77.1% occurrence. Although nest sites were located in drier microhabitats, large expanses of dry ground were avoided as were the wettest low relief meadows and marshes.

Semipalmated sandpiper

Semipalmated sandpipers nested mainly in mesic vegetation types of low relief (Table 14). Nests occurred in all but the wettest and driest vegetation types, but the greatest concentration occurred in low and medium relief lcp and terraced slope. No nests were found in tussock slope, high center polygons or Arctophila marsh. The high preference ratio for high relief lcp is questionable because of the

low expected value. Nest site characteristics (Table 15) show that, as with longspurs, the microhabitat of the nest site itself differs somewhat from the range of cover values and species composition found in the surrounding vegetation type, being drier on the average. Unlike the situation for longspurs, no plant species is structurally necessary for the sandpiper nest scrapes, and plant species composition is indicative only of the general nature of microhabitat preference. Semipalmated sandpiper nest sites averaged somewhat drier with more diversity in plant species than those of the other common sandpipers. C. aquatilis cover averaged 54.1%, slightly less, and total Salix spp. averaged 16.0%, slightly more than for pectoral sandpipers and red-necked phalarope nest sites. Heath species occurred in 85.7% of nest site plots, with D. integrifolia the most significant heath associate. S. reticulata had a high frequency of 95.2%, equal to that of S. arctica. C. bigelowii had a higher frequency of occurrence (14.3%) at semipalmated sandpiper nest sites than at those of other common sandpipers. In general, semipalmated sandpipers nested in dry microsites in low to medium relief, mesic vegetation types.

Pectoral sandpiper

The distribution of pectoral sandpiper nests was similar to that of semipalmated sandpipers, with most nests occurring in dry meadow, medium relief lcp and terraced slope vegetation types. Nests were too few to provide conclusive information on vegetation type preferences, but within these types, pectoral sandpipers appeared to utilize

slightly wetter microsites than did semipalmated sandpipers, perhaps the result of less specificity in nest site requirements. The average number of plant species per m^2 was lower (10.1), and average moisture index higher (2.1) than for semipalmated sandpiper sites. Cover of C. aquatilis (63.6%) was higher than at semipalmated sandpiper nest sites. D. integrifolia occurred in 63.6% of plots and S. reticulata in 72.7%. Pectoral sandpiper nest site characteristics did not differ greatly from those of semipalmated sandpiper nest sites, but were consistently indicative of slightly wetter sites.

Red-necked phalarope

Only 7 red-necked phalarope nests were found, but their distribution appeared to indicate preference for even greater moisture at the nest site than was true for pectoral sandpipers (Table 15). Although overall a drier vegetation type, the occurrence of red-necked phalarope nests in high center polygons is typical, as high center polygons are characterized by a high frequency of small ponds and surrounding wet Carex. The average moisture index, 3.3, indicates a wet site, as does the low average number of species per plot, 8.0. Red-necked phalarope nests were invariably located in tall Carex, with average height of vegetation (36 cm) much greater than that found at nest sites of the other sandpipers studied. Cover of C. aquatilis was high (64.2), and E. angustifolium, which is characteristic of wet sites, had an average cover value of 5%. Total graminoid cover (82.2%) was higher and total woody cover (10.0%) lower than at nest sites of other bird species. Frequency of occurrence values show a

high incidence of species typical of wet sites: C. aquatilis, 100%; D. fischeri, 50%; E. angustifolium, 33.3%.

Other species

Other species nests were too few for analysis. Red phalaropes nested in very wet areas of low relief and were more common at locations approximately 3 km inland, where several large drained lake basins provided expanses of wet meadow and low relief lcp. Willow ptarmigan nested in mesic polygonized terrain and rock ptarmigan in uplands. Sandhill cranes were rare and only one pair was present each year in the study area, with a nest in medium relief lcp. Oldsquaw nested on dry polygon ridges and among larger willows, sometimes a great distance from water. Baird's sandpipers were uncommon and the 2 nests reported here were in dry centers of high center polygons very near the coast. Red-throated and arctic loons were found throughout the study area, with one pair of loons for every suitable lake or pond. The arctic loons were less common and restricted to larger bodies of water. Stilt sandpipers nested commonly in dry microsites of medium to high relief areas. Although buff-breasted sandpipers were common during lekking displays, only one nest was found on the study area. Common eiders, whistling swans, lesser golden-plovers, black-bellied plovers, parasitic jaegers, glaucous gulls, arctic terns, semipalmated plovers and snow buntings also nested in the study area.

D. Density

Estimates of nest density on the 30-ha study plot are presented in Table 16. Probable renest attempts of known nests are excluded from the estimates. However, the asynchronous nature of nest initiation in 1978 makes positive identification of renests difficult (Fig. 11). In cases where a late nest was initiated within about 70 m of a known nest of the same species which failed between 3 and 5 d earlier, the nest was considered a renest. Such nests were not included in density estimates. Late nests which were not located in the vicinity of a recently failed nest were included.

Nest densities on the study plot appear comparable to those found in other regions of the eastern North Slope of Alaska (Table 17). Of coastal sites studied, the densities are most similar to those of Martin and Moitoret's (1982) "mosaic" habitat plot near the Canning River in the ANWR and Hohenberger et al.'s (1980, 1981, 1982) "wet coastal plain" plot south of Prudhoe Bay. However, caution should be exercised in comparing studies. Local variation in nesting densities of some common species appears to be high, as is yearly variation. Several studies have demonstrated distinct vegetation type preferences for all the bird species considered here (in particular, see Troy et al. 1983). Hence the accuracy of densities extrapolated from single plots with an unknown or non-representative distribution of vegetation types to nests/km^2 is doubtful. The number of plots used and the area sampled by Troy (1982) and Troy et al. (1983) would provide the most accurate of the estimates of density presented in Table 17.

Table 16. Bird nest densities (nests/km^2) on the 30-ha study plot at Demarcation Bay, Alaska. Number of nests in parentheses. Codes are as defined in Table 1.

		Vegetation types							
	Total	M	LR	MR	HR	TS	HCP	CP	DIST*
All Species									
1978	123.2	30.1	167.4	129.3	-	88.3	100.0	-	211.0
	(37)	(1)	(19)	(3)	(0)	(4)	(5)	(0)	(5)
1979	136.7	120.5	149.8	86.2	-	198.7	100.0	-	42.2
	(41)	(4)	(17)	(2)	(3)	(9)	(5)	(0)	(1)
Lapland longspur									
1978	40.0	0.0	52.9	0.0	-	44.1	60.0	-	42.2
	(12)	(0)	(6)	(0)	(0)	(2)	(3)	(0)	(1)
1979	66.7	0.0	70.5	43.1	-	110.4	80.0	-	0.0
	(20)	(0)	(8)	(1)	(2)	(5)	(4)	(0)	(0)
Semipalmated sandpiper									
1978	33.3	0.0	44.0	129.3	-	44.1	0.0	-	0.0
	(10)	(0)	(5)	(3)	(0)	(2)	(0)	(0)	(0)
1979	33.3	30.1	52.9	0.0	-	44.1	0.0	-	0.0
	(10)	(1)	(6)	(0)	(1)	(2)	(0)	(0)	(0)
Pectoral sandpiper									
1978	33.3	0.0	44.0	86.2	-	0.0	0.0	-	126.6
	(10)	(0)	(5)	(2)	(0)	(0)	(0)	(0)	(3)
1979	6.7	0.0	0.0	0.0	-	44.1	0.0	-	0.0
	(2)	(0)	(0)	(0)	(0)	(2)	(0)	(0)	(0)
Red-necked phalarope									
1978	13.3	0.0	17.6	0.0	-	0.0	20.0	-	42.2
	(4)	(0)	(2)	(0)	(0)	(0)	(1)	(0)	(1)
1979	10.0	30.1	17.6	0.0	-	0.0	0.0	-	0.0
	(3)	(1)	(2)	(0)	(0)	(0)	(0)	(0)	(0)

* Not mappable from aerial photography.

Table 17. Estimates of nest density (nests/km^2) from regions of the eastern north slope of Alaska. Numbers are averages where more than 1 year's data are available, ranges are given in parentheses.

	Shorebirds	Longspurs	Total nests
Demarcation Bay[a]			
1978 and 1979	70 (57-83)	45 (37-53)	121.5 (120-123)
Okpilak River Delta[b] 1978 and 1982			
Flooded	29 (20-38)	11 (10-12)	49.5 (38-61)
Mosaic	34 (28-40)	48 (41-55)	86 (85-87)
Wet sedge	23 (14-32)	30.5 (29-32)	55.5 (45-66)
Sedge-tussock	10 (8-12)	44 (40-48)	58.5 (49-68)
Canning River Delta[c]			
Upland 1979 and 1980	35 (31-39)	27.5 (20-35)	64.5 (51-78)
Lowland 1979 and 1980	57.5 (48-67)	16.5 (11-22)	76 (59-93)
Mosaic 1980	74	51	137
Prudhoe Bay			
IBP sites[d]			
1971 and 1972	89 (87-91)	8 (7-9)	96.5 (93-100)
Wet Coastal Plain Tundra[e]			
1979 to 1981	84 (74-101)	45.3 (44-47)	137 (126-152)
Waterflood Project[f] 1981 and 1982			
Experimental plot	52.5 (51-54)	15.5 (14-17)	73.5 (71-76)
Control plot	42.5 (40-45)	17 (17-17)	65 (64-66)

[a] This study.
[b] Spindler 1978, Spindler and Miller 1982.
[c] Martin and Moitoret 1982.
[d] Norton et al. 1975.
[e] Hohenberger et al. 1980, Hohenberger et al. 1981, and Hohenberger et al. 1982.
[f] Troy 1982, Troy et al. 1983.

However, their methods (not designed specifically for estimation of density) probably produced underestimates due to missed nests, particularly failed nests.

For the Demarcation Bay study area, the densities in Table 16 may be representative for Lapland longspur, semipalmated sandpiper and pectoral sandpiper in the most common vegetation types. The exclusion of red phalaropes from the study plot makes the total density for meadow and low relief lcp vegetation types low. Red phalarope nests were common in expansive wet meadows further inland. Other species were also common in the rare vegetation types; e.g. loons, tundra swans, and glaucous gulls in Arctophila marshes, and lesser golden-plovers in medium to high relief lcp and high center polygons. Accurate estimates of nest density for these and other low density species (stilt sandpiper, black-bellied plover, arctic terns, oldsquaw, common eider, Baird's sandpipers, long-tailed jaegers, willow and rock ptarmigan) are extremely difficult to obtain.

ARCTIC FOX INVESTIGATIONS

I. RESULTS

Six foxes were captured and fitted with radio-collars between 12 May and 13 June 1979. Victor leg-hold traps, which were used between 12 May and 9 June, captured 3 foxes. Wire-mesh box traps were used between 9 and 13 June, and captured another 3 foxes. The wire-mesh box traps were deemed superior for several reasons. Although the jaws were offset on the Victor traps, the first fox captured lost a hind foot. Padding the jaws with fiber tape prevented major injury to the other 2 foxes captured in Victor traps, although some wounding to both legs and teeth still occurred. In addition to causing injuries, these traps were difficult and time-consuming to set and became ineffective during cycles of rain or heavy mist and freezing weather, which froze the sand over the trap spring during May and early June. The wire-mesh box traps were easy to set and could be placed anywhere on the tundra. The Demarcation Bay foxes were doubtless inexperienced with traps of either variety, accounting for their ease of capture. Sardines were used as bait for both types of trap.

Fox 1, a male, lost a hind foot and severely injured a front paw in a leg-hold trap on 12 May. Between 12 and 20 May he was seen on several occasions resting with another fox on top of a den and moving slowly about the general vicinity of the den. Tracks of a 3-legged fox were seen approximately 3 km east of the den indicating that he was moving some distance away from the den during this time. He was not seen and could not be located by radio from the ground between 20 May and 5 June,

when a signal was picked up from the shore-fast ice and he was located not far offshore. Observations at that time indicated that near-shore ice ridges completely attenuated the line-of-sight radio signal. On 7 June, Fox 1 was captured again in a leg-hold trap. He was uninjured and his previous wounds appeared to be healing. He was able to move about fairly well on 3 legs at that time. He again disappeared, however, and was not relocated until 21 June when he was seen near our camp without his radio-collar. We were unable to locate the radio and no additional collars were available. Although we could not track Fox 1, he was observed while tracking his mate, Fox 3, and he often approached within 2 m of observers to whom he seemed to pay little attention.

Fox 2 (male) was captured, collared and released 13 May and was never relocated. Fox 3 (female and mate to Fox 1) was captured 31 May, and was one of 2 collared foxes which remained in the area, retaining a functional radio-transmitter throughout the summer. Fox 4 (male) was captured 11 June and followed for 24 h. Apparently dispersing through the area, he headed west along the coast and was never relocated. Fox 5 (female) was radio-collared 12 June and was resident in the area throughout the summer. Fox 6 (male) was captured 13 June and followed for several hours after release. He moved south and out of the study area, and was relocated to the southeast of the study area on several occasions later in the summer. Subsequent to the 13 June observations, sightings of Fox 6 were made only once, when he was seen moving deep into the study area from the southeast and then returning.

Foxes 3 and 5 were tracked during 38 systematic tracking shifts. Behavioral observations of Foxes 3 and 5 and of any other foxes encountered were made whenever we were within approximately 100 m of the animal being observed during the tracking period and on 16 occasions when foxes were encountered while we were not actually tracking. The distribution of hours of tracking and observation among 10-d periods is presented for each fox in Table 18.

Although sampling was designed to provide systematic tracking data for continuous 8-h periods, actual tracking periods ranged from only 3 min to 9.5 h. This was due to many factors including weather, equipment failure, observer experience and rate of movement of the fox. Weather was the most significant factor influencing the number of hours of tracking in a period; many tracking shifts were terminated due to fog. The low number of hours of tracking in the period 8/5 to 8/17 was due to nighttime darkness in mid-August during which observations and tracking became impossible.

Foxes were tracked a total of 266.2 h; most effort was concentrated on Foxes 3 and 5 with 107.5 and 144.3 h of tracking, respectively. This is 6.9% of the total of 1560 h between 14 June and 17 August for fox 3 and 11.1% for fox 5. Direct observation records are somewhat less: 184.8 h total, with 12.1 h for male foxes and 172.7 h for female foxes. The ratio between hours of observation and hours of tracking of Foxes 3 and 5 is a measure of the efficiency of the tracking method in obtaining behavioral observations. The ratios vary little between foxes or periods and indicate an overall efficiency near 70%, i.e. approximately

Table 18. Seasonal distribution of hours of tracking and hours of direct observation of arctic foxes at Demarcation Bay, Alaska in 1979.

	Fox 1	Fox 3	Fox 5	Fox 6	Fox 7*	Total	Ratio
14-25 June							
Observation	0.55	14.57	15.44	0.14	5.70	36.40	0.69
Tracking	0.55	21.07	24.27	0.15	6.21	52.24	
26 June-6 July							
Observation	2.19	8.45	17.73	0.20	0.14	28.72	0.71
Tracking	2.17	13.25	24.60	0.20	0.13	40.35	
7-16 July							
Observation	0.27	13.53	16.21	0.13	0.97	31.11	0.69
Tracking	1.32	19.25	23.40	0.13	0.98	45.08	
17-25 July							
Observation	0.86	16.89	15.84	-	-	33.60	0.65
Tracking	1.35	21.63	28.90	-	-	51.88	
25 July-4 August							
Observation	-	9.50	18.42	-	0.90	28.81	0.72
Tracking	-	14.30	24.50	-	1.02	39.82	
5-17 August							
Observation	0.07	12.59	13.53	-	-	26.19	0.72
Tracking	0.08	18.03	18.68	-	-	36.80	
Total							
Observation	3.95	75.53	97.17	0.48	7.71	184.83	0.69
Tracking	5.47	107.53	144.35	0.48	8.34	266.17	
Ratio	0.72	0.70	0.67	0.37	0.92		

* Fox 7 is an uncollared adult male, mated to Fox 5.

30% of each 8-h shift was spent catching up to foxes which had moved beyond the defined range for observation.

The higher variability in hours of observation each period and the lower total number of hours of observation for Fox 3 (Table 18) are due to a combination of factors, including weather on days when she was tracked and a more distant home range. Although our efficiency for Fox 3 was higher than for Fox 5, Fox 3 seemed more difficult to track due to differences in behavior (see Section II. Discussion) and this may have contributed to the differences in hours of observation for Foxes 3 and 5.

The distribution of minutes of observation per hour of day is presented in Fig. 13. Although efforts were evenly distributed among hours, the "nocturnal" activity pattern of the foxes (see Section II, B. Activity Patterns) resulted in a much greater efficiency of observation during inactive periods in mid-day. No differences in the distributions of minutes of observation per hour of day between periods were detected (Smirnov test, $p>0.05$). Similarly, no significant differences in period means of minutes of observation per hour of day were detected (Kruskal-Wallis test, $p>0.05$). These statistics indicate that neither the observer's ability to make observations nor the nocturnal activity pattern of the fox changed between 13 June and 18 August. However, continued observations of nocturnal activity after 18 August were impossible due to rapidly decreasing day length.

The average duration of a sighting was 34 min. No significant differences in sighting durations between Foxes 3 and 5 were detected

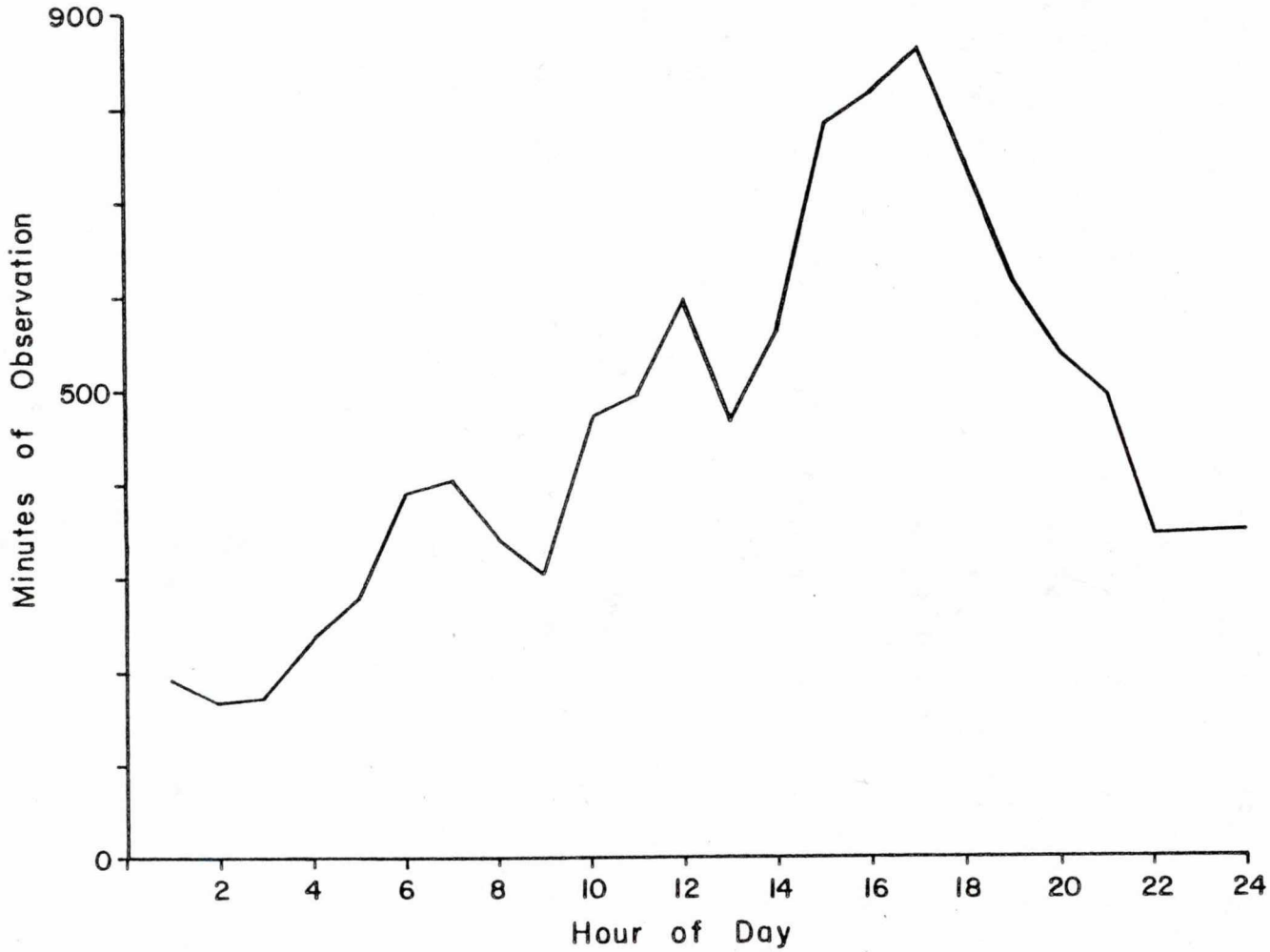

Figure 13. Hourly distribution of total minutes of direct observation of arctic foxes at Demarcation Bay Alaska in 1979.

(Mann-Whitney test, $p>0.05$), nor were any significant differences in sighting durations detected between periods (Kruskal-Wallis test, $p>0.05$). These statistics indicate that the foxes were equally observable, and ability to make observations did not change between 13 June and 18 August.

The directional antennas on 9-m masts were inadequate for triangulating the locations of foxes because mast locations were poorly chosen for monitoring the home ranges encountered. None of these data were accurate enough to describe fox movements, activity patterns or habitat use, and they are not presented here.

II. DISCUSSION

A. Behavior descriptions

The behavioral repertoire of arctic foxes has been described by Fox (1969, 1970, 1971), Speller (1972), Caley (1972) and Fine (1980). An annotated outline of arctic fox behaviors recognized in this investigation is presented here. The relationship between the behaviors recognized for the purposes of this investigation and previously described "ethograms" is indicated in the discussion. To organize this presentation, I have divided arctic fox behaviors into 4 major categories: 1) movements, 2) foraging activities, 3) social activities, and 4) maintenance activities. Behaviors recorded for analysis of activity patterns and activity budgets are underlined.

This undoubtedly represents only a small fraction of the behavioral repertoire of arctic foxes. Many more hours of observation will be

required for a reasonably complete analysis of arctic fox behavior. This investigation provides some insight as non-breeding mated adults have not been observed in previous behavior studies.

Movements

Searching refers to the most commonly observed movement patterns of an undisturbed arctic fox. Searching corresponds to Fine's (1980) movement pattern, "forage". Although foraging is probably the usual purpose, foxes appear to search out and react to various stimuli when searching, including scent-marks and unusual or unfamiliar objects. In addition, the regular movements of a fox through its home range may serve other social purposes. While most other activities are of very short duration, searching occupies nearly 75% of the foxes' waking hours. Although the movements of a searching fox appear random, with frequent changes of direction at intervals of 30 s or less, foxes gradually move in one general direction through an area when searching. Searching arctic foxes move in a characteristic loping trot intermediate in speed between running and walking. Foxes search with heads lowered, apparently searching for or responding to scents, sounds or visual stimuli.

Slow searching occurs when a fox stops, with nose to the ground, and investigates an area several meters in diameter. Alert postures (i.e. forward-directed ears and raised tail) are exhibited, and the animal continues to move slowly at intervals, perhaps returning to the site of initial interest. Slow searching may be followed by searching, pursuit or capture of prey, scent-marking, retrieval of a cache,

rolling, or an intraspecific encounter. These sequences indicate that, like searching, slow searching need not be directly related to procurement of food. The fox may be investigating the scent mark of another fox, some other particularly attractive odor, or a potential rest site. Slow searching corresponds to Speller's (1972) "intensity 2 hunting."

Travel is a more or less straight-line, rapid movement of a fox toward some single goal. Fine (1980) typified travel as the movement of an adult fox carrying food to the den. The difference between searching and travelling is one of degree, though the 2 are usually easily distinguished by the rate of progress and posture. Speller (1972) observed denning foxes to travel directly to and from hunting areas along specific routes. Travelling was rarely observed in this investigation due probably to the fact that foxes had no pups to which to carry food and lacked regularly used resting or foraging areas. Travelling was recorded occasionally when a searching animal would stop, increase pace and move with head raised and without pause, although the stimulus was usually unknown. This typically resulted in the termination of an observation bout as the animal moved away and observers attempted to follow.

In addition to searching, slow searching and travel, foxes occasionally exhibited a leaping gait, similar to the "stotting" behavior of antelope. Such behavior was observed during intra-specific agonistic encounters when an interloper began to run from a territorial

fox. It was also observed when a fox encountered a human or a caribou unexpectedly, and upon release of a fox following radio-collaring.

Swimming was observed rarely, though the foxes showed no hesitation to swim. After a brief shaking when getting out of the water, they appeared quite dry. Foxes were observed on several occasions swimming between small islands in a coastal pond or lake, presumably searching for (and frequently finding) nests of waterfowl, loons, gulls, or terns.

Foraging activities

Pursuit occurred whenever live prey items were encountered. Four specific behaviors were exhibited in pursuit: 1) stalking, 2) chasing, 3) digging, and 4) pouncing. No pursuit occurred with predation of nests. With other avian prey the outcome of pursuit was determined nearly instantaneously; rarely was there a protracted period of stalking. With small mammals, a pursuit episode typically had a greater duration; digging was often particularly prolonged. An encounter with a small mammal was followed by a brief chase in a quick zig-zag course which covered very little ground, and ended in a pounce. The pounce was either accompanied by a biting attack or followed by digging if no capture was made. Pounces were repeated at intervals by digging foxes and are also described by Speller (1972) who recognized "leaping" as a separate behavior. Any of these behaviors may be preceded by "freezing" (Speller 1972), where the fox stands still in a semi-crouch with tail extended, head low and ears perked and facing forward. In addition, Speller defines "lunging" and "dashing," both variations on chasing. According to Speller, the various pursuit techniques used vary through a

season and between habitats as prey distribution and types of prey hunted vary.

Capture was recorded as a behavior in order 1) to enumerate successful pursuits and discovery of nests, 2) to distinguish these from discovery of caches, and 3) to compare rates of caching and eating per capture.

Eating was recorded for any food item actually consumed. For most prey animals there was virtually no kill time and consumption of prey was equally quick. At a large carcass, eating bouts were protracted and the foxes would glut themselves and carry off some meat for caching. Some caches appeared to consist of partially-digested food suggesting that the animals gorged themselves and then regurgitated food in caches before returning to the carcass. Observations of foxes feeding from a carcass also suggested that foxes were consuming much more meat than could be processed in many hour-long feeding bouts. These were followed by forays of similar duration away from the carcass, and the sequence was repeated until no meat remained. Such activity sometimes lasted for 30 to 50 h.

Caching of food occurred in every 10-d period. Five types of behavior are associated with caches: 1) carrying food, 2) digging the cache hole, 3) cache and cover, 4) returning to the source, and 5) cache retrieval. Food and non-food items (including plastic and decaying bird parts, such as wings) were usually cached 20 to 50 m from their original location. Occasionally large food items, such as large eggs, were carried much farther. When carrying a cache item, the fox searched in a

deliberate manner for a cache site, often testing several sites before actually making the cache. Most cache holes were mere scrapes where the turf or moss was pulled toward the fox with the forepaws. A cache was made by the fox by placing the item in the scrape and using its nose to push back the displaced turf. There was rarely, if ever, any landmark associated with a cache location and the characteristics of a cache site are poorly defined. If more food remained the fox returned to the source (not always directly), and repeated the sequence.

The location of a cache bore no obvious relation to locations of previous caches. I never observed a fox to place more than one item in an individual cache. The fox frequently urinated on a nest site after removing the eggs, but cache sites themselves were never marked with urine. From my observations, caches were rediscovered opportunistically, as were nests and other food items, by sight or scent. When searching, a fox may orient suddenly toward some location, sniff around briefly and then uncover an egg or other food item. Retrieved food items were either eaten immediately, or, quite frequently, carried up to approximately 100 m away and recached. It is likely that many of the caches I observed foxes to retrieve were originally made by another fox. Retrieved non-food items were typically rolled on or played with and then recached.

Caching behavior apparently differs somewhat in denning foxes, which may cache several lemmings temporarily at one location to be retrieved on the return trip to the den (Speller 1972). Such caches are definitely short-term and result simply from not being able to hunt and

carry food at the same time. Speller (1972) reports that the largest number of lemmings a fox appears to be able to carry at one time is 7 or 8. Caching behavior I observed was quite different. Nearly half of the caches observed in this investigation were of single shorebird or waterfowl eggs. All caches were dispersed and retrieved, if at all, one at a time and at a much later date.

Scent-marking is both a social and a foraging activity; an analysis of its functional significance is made in the discussion of activity patterns. Although defecation and deposition of scent from specific glands are, strictly speaking, forms of scent-marking, use of the term here refers to urinations only, as they alone were observed frequently enough for analysis. Arctic foxes of both sexes scent-mark frequently; however, insufficient observations of males do not allow comparison of sexes. Males scent-mark in a squatting position, or they may raise one leg to urinate on an upright object. Females scent-mark in a squatting position. My observations generally agree with the conclusions of Henry (1977) on the function of some scent-marks for foraging in red foxes. Rather than marking boundaries and fulfilling an agonistic social function, the primary purpose of some marks in arctic foxes is to increase foraging efficiency for the regular user of the territory, indicating perhaps how recently a particular area has been visited. No analysis was possible of the frequency of scent-marking after or during intraspecific encounters, or on territory boundaries as opposed to more exclusively used areas. I do not have data from the mating season when scent-marking may serve other primary functions (Bailey et al. 1980).

Social activities and play

Arctic foxes form mated pairs in which both male and female take an active part in rearing of pups. Speller (1972) demonstrated that in order to achieve their full reproductive potential, a mated pair of arctic foxes must maintain a strong family bond throughout the denning season. My observations indicate that non-breeding arctic foxes also maintain a pair bond during the summer and that mated pairs cooperate in establishing and defending summer territories. Although tolerance for conspecifics is low, the pair bond is reinforced by interactions between members of a mated pair and, when pups are present, between adults and pups. In winter, arctic foxes are solitary; however, they do not defend a territory and their tolerance for conspecifics may be higher than during summer. Many reports of winter concentrations of arctic foxes have been made (Chesemore 1968b) and this may be the season of the highest rate of social contact for those individuals which concentrate near large food sources such as large mammal carcasses (whale, seal, walrus or caribou) and garbage dumps.

I have divided social activities into 3 categories: 1) non-agonistic interactions and play, 2) agonistic encounters, and 3) vocalizations. The first category includes: greeting postures, solitary play, and social play. Agonism occurred between mates, between resident foxes and trespassing foxes, and between foxes and other species. Agonistic encounters consisted of chasing and escaping. Vocalizations are many and varied, as predicted by Fox (1975) for solitary-hunting canids, though most of their functions remain unknown.

a) Non-agonistic interactions and play

Members of a mated pair occasionally foraged or rested within several meters of one another for extended periods without obvious communication or interaction, although they were certainly aware of one another. Greeting postures occurred when members of a mated pair encountered one another at any location in their home range. Either the male or female fox would initiate greeting by approaching the other at a walk or slow gait. If the other fox was aware of its approaching mate its response was usually to sit and avert its gaze with ears lowered. Greeting postures occasionally led to social play, but were often followed by resting of one or both foxes or simply continuation of foraging behaviors after acknowledgement.

Play behaviors of pups and between adults and pups are described by Caley (1972) and Fine (1980). Play also occurs between adults and in solitary adults. Solitary play was observed on several occasions in very brief bouts. In one instance an adult female found a plastic coffee can lid, pounced and picked it up. She then ran very swiftly with the lid in her mouth making several quick turns and tossed the lid on the beach. She retrieved the lid, dug a hole and buried it in the sand. A similar sequence was observed of an adult female with the decomposing wing of a goose. In addition, there were several periods of rolling and deliberate rubbing of the shoulders on the wing before caching it among tussocks approximately 100 m from where it was picked up.

Social play appears to have 3 components: 1) play invitation postures, 2) chases, and 3) wrestling. In my observations social play between 2 foxes was always preceded by greeting and play invitation. If play was to follow, greeting postures were typically brief and the foxes often appeared excited. A typical canid play invitation posture was usually assumed by one fox before play. Such a begging posture frequently elicited no response. In those cases the invitation posture would be repeated, or followed by walking slowly towards the mate or sitting with gaze averted. Positive responses by the mate to the play invitation included assumption of the play invitation posture, a sudden dash toward or away from the solicitor, or rolling over on the back while vigorously shaking the tail.

Chasing occurred when a fox responded to an approaching playmate by dashing away. Chases were very fast with many changes of direction and also with frequent switching of roles similar to a game of tag. Chasing play was also observed between single foxes and caribou. In one instance, a fox approached a small group nonchalantly, moving in a manner typical of a hunting fox. When within approximately 20 m of a caribou, the fox suddenly burst into a very fast run directly toward that animal, then suddenly turned 60 to 90 degrees, dashing around between animals within the group, changing directions frequently and suddenly. The fox often came within several meters of a caribou before turning. Reactions of caribou varied. Typically the caribou were alert and aware of a fox before it began running. They startled briefly when the dash began or when approached very closely. Usually the group

tightened and animals stood closer together. Only 2 animals, in one instance a lame cow and, in another instance, a calf, were observed to run in response to an approaching fox. The lame animal ran to get away and was obviously very nervous even as the fox approached. The response of the calf appeared as playful as the behavior of the fox. In this instance, the fox dashed between a cow and calf; the calf darted away as the fox passed, then stood. The fox then circled and ran directly toward the calf, which took off at top speed, easily outdistancing the fox and circling about 300 m around the herd. When the calf had gained several hundred meters it stopped, looked back and waited for the fox to approach again before taking off. This sequence was repeated several times before the fox slowed to a lope and finally laid down, apparently exhausted. After several minutes the fox again approached the calf, slowly and nonchalantly, looking the other direction, then dashed at it, but the fox failed to follow up in the chase and initiated searching movements. A fox-caribou encounter is also described by Fine (1980).

Wrestling was initiated when a fox raised up on hind legs to meet an approaching animal. The 2 foxes stood together with forepaws on each other's shoulders and biting each other's faces or necks until they toppled over. Wrestling continued on the ground, with the animals rolling and pouncing until one fox rolled onto its back. The "victor" typically stood directly over or on top of the other fox with its gaze averted for several moments, although the "submissive" fox often used this moment for a renewed attack.

Play was generally terminated by both animals quite suddenly at some unrecognized cue and they would then depart the area in different directions (although their paths might coincide for a period). Play behaviors occurred at any location, as there was no center of activity in these non-breeding foxes. There were no apparent seasonal patterns in the occurrence of play or in encounters between members of a mated pair; however, non-agonistic interactions were not frequently observed. Play occurred in less than 5% of the observed encounters between mates.

b) Agonistic interactions

Territorial agonistic behaviors between foxes consisted of chasing and escaping. Although ranges overlapped throughout the season, the roles of the foxes in agonistic encounters were unquestioned in all instances, and no fighting was observed. The interloper, if aware of the dominant or resident fox, would run in a leaping gait (described in Section II, A. Behavior Descriptions) for several tens of meters before breaking into a run. A resident fox when aware of the interloper would run directly at the other fox. The ensuing chases typically lasted about 30 s, but one lasted 5 min and another lasted 21 min. The chases typically consisted of several fast bursts with the chasing fox slowing first. If the fox continued to run away, the interaction ended; if not, the pursuer continued the chase. The escaping foxes' reaction may determine the duration of the interaction. No physical contact was observed in any territorial interaction.

Agonism between members of a mated pair was observed only when one fox was feeding from a carcass or cache. The duration was always brief but was frequently repeated as the other fox attempted to feed. The episodes consisted of growling, baring of teeth, and lunging at the intruder when approached too closely while eating. At a caribou carcass only one member of a pair was able to feed at a time. As long as a fox was feeding it defended the carcass from its mate. When the defending fox was finished, it moved away and roles were suddenly reversed. On no occasion did an approaching fox drive away a feeding fox; the aggression was consistently on the side of the feeding member of the pair regardless of sex. Attacks of this type were usually directed at the face or muzzle of the other fox whose reaction was either to yelp and escape or to stand momentarily, mouth wide against the attack before moving back slowly. On one occasion similar aggression occurred when, during a bout of play, a female fox discovered a cache and began to eat. The male, continuing to play, ran to the female, placing a paw on her back. The female's reaction was immediate and unquestionably aggressive. The male retreated some distance and when the female finished eating she promptly initiated another play bout.

A final type of social interaction is interspecific agonism, which was observed considerably more frequently than interactions between foxes. Mobbing by short-eared owls, glaucous gulls, arctic terns and jaegers was at the least annoying to arctic foxes and on occasion caused the fox to flee. Mobbing by larger shorebirds was typically ignored although foxes frequently snapped or leaped at diving birds. Adult

caribou, although they typically were unconcerned, occasionally charged foxes.

c) Vocalizations

Vocalizations of arctic foxes are many and varied. Although Fine (1980) distinguished play from agonism by its lack of vocalizations, my observations indicate both play and agonism are regularly accompanied by frequent and quite similar vocalizations of variable intensity. Because I was often unable to ascribe functions to particular vocalizations, I mention them separately here, rather than in association with other behaviors. Six general vocalizations are recognized by Fine (1980): 1) "barking," 2) "squealing," 3) "yelping," 4) "rumbling," 5) "staccato barking," and 6) "wailing." Barking is attributed an alarm function by Fine (1980) and may also be a weak threat, being heard at dens or when a resting fox is approached by another fox or caribou. Squealing was attributed by Fine only to pups and was not observed in this study. In this study, yelping was invariably associated with fear, pain, or submission, occurring both during play and agonism. I interpret Fine's "rumbling" as growling, which occurs during wrestling play and during agonism when foxes are in close quarters, and functions as a threat. The staccato bark is the most common fox vocalization heard on the tundra and often answered by other foxes. As mentioned by Fine (1980) it seemingly served to announce one's presence to other foxes. Wailing is an eerie loon-like call heard infrequently. On several occasions a wail call in the distance preceeded observation of a social encounter

between members of a fox pair. The vocal repertoire is undoubtedly larger and more subtle than recorded here and vocalizations were no doubt made more frequently than they were recorded during this investigation. Observations made in the continual wind of the North Slope and at some distance from the foxes made vocalizations difficult to percieve.

Maintenance activities

Maintenance activities include sleeping, resting, scratching, grooming, rolling, sitting alert, and defecating. I did not distinguish between sleeping and resting prone, as foxes are light sleepers without prolonged periods of deep sleep and, when prone, were often not visible. Defecation may have some yet undefined social significance as scent stations of feces are often reported for arctic foxes (Kleiman 1966). Failed nests were frequently found with fox feces in the nest bowl.

B. Activity patterns

The arctic fox maintains a definite 24-h activity cycle in a distinctly nocturnal pattern throughout the summer period (Fig. 14). Arctic foxes typically became active around 1800 h. The activity period usually ended between 0800 and 0900 hours. Occasionally, one or several brief rests of 0.5 to 1 h occurred; typically, a resting bout occurred around midnight. The number and cumulative duration of resting bout during the night depended to some extent on weather; heavy rains in particular caused lower levels of activity. Activity bouts were not at all uncommon at mid-day but these were usually of short duration.

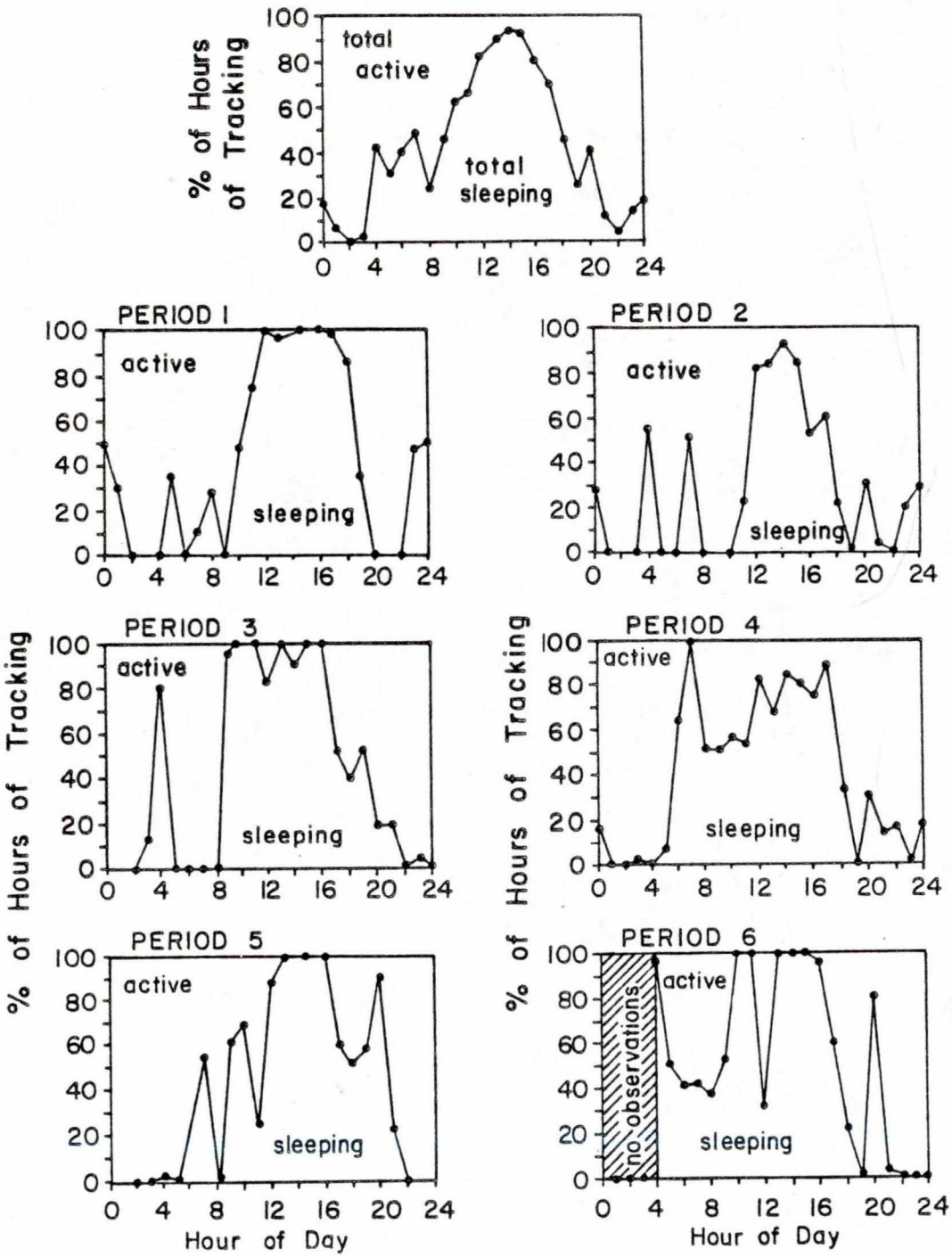

Figure 14. Activity patterns of arctic foxes at Demarcation Bay, Alaska between 14 June and 17 August, 1979. Period durations are: period 1, 6/14-25; period 2, 6/26-7/6; period 3, 7/7-16; period 4, 7/17-25; period 5, 7/26-8/4; period 6, 8/5-17.

Fig. 14 shows no seasonal trends in the basically nocturnal pattern over the duration of the study.

Mean durations of resting and active bouts are presented in Table 19. The average duration of a resting bout was 1.7 h (SD=2.32). The longest resting bout recorded was 8.42 h and the shortest 1 min. Because of frequent brief changes of position, grooming, and alert behaviors during rest periods, such active periods of 5 min or less were ignored in calculating resting bout durations. The distributions of resting bout durations differ significantly among 10-d periods (Kruskal-Wallis test, $p<0.05$). It appears that resting bout durations were greatest in the period 6/14 to 6/25, and shortest in the period 7/17 to 7/25 (Table 19).

The average duration of an activity bout was 1.4 h (SD=1.90). The shortest activity bout recorded was 3 min and the longest was 7.87 h. Activity bouts were longest in the period 7/17 to 7/25 and shortest in the periods 6/26 to 7/6 and 8/5 to 8/17.

The proportion of hours of tracking active and resting foxes in each 10-d period is also presented in Table 19. Foxes were active during 55% of 266.17 h of ground tracking. Period 6 is biased toward resting because nighttime tracking was curtailed between 2400 and 0400 h.

The periods 6/14 to 6/25 and 7/7 to 7/16 show the greatest proportions of resting time. The period 6/14 to 6/25 is characterized by long duration resting bouts and a low proportion of active behaviors in the total activity budget. The period 7/7 to 7/16 includes many

Table 19. Hours of tracking of active and resting foxes at Demarcation Bay, Alaska in 1979 and mean durations of active and resting bouts each period. Only activity and resting bouts with known duration are used.

	Tracking periods						
	6/14-25	6/26-7/6	7/7-16	7/17-25	7/26-8/4	8/5-17	Total
Hours resting	24.29	16.14	20.74	21.79	17.12	20.79	119.78
Hours active	27.94	24.21	24.34	30.09	22.70	16.01	146.39
Proportion resting	0.46	0.40	0.46	0.42	0.43	0.56	0.45
Proportion active	0.53	0.60	0.54	0.58	0.57	0.43	0.55
Ave. resting bout	2.16	1.46	1.88	1.27	1.54	1.57	1.68
(SD)	(2.66)	(1.99)	(2.15)	(1.98)	(2.27)	(1.41)	(2.32)
Ave. activity bout	1.54	1.19	1.22	1.89	1.75	1.21	1.44
(SD)	(2.19)	(1.81)	(1.86)	(1.93)	(2.39)	(1.14)	(1.90)

hours of observation of a fox pair feeding on a caribou carcass, from which neither fox moved a very great distance until the meat was gone. During those tracking shifts, both foxes were glutted and inactive for long periods. Excluding the period 7/7 to 7/16, activity levels appear to have remained stable, or to have increased slightly from 14 June to 4 August.

None of the measures of activity patterns presented above showed a distinct relationship with patterns of food availability. The period of greatest food availability was the nesting season, approximately 5 to 23 June in 1979 (Fig. 12). Outside the study plot, the rate of predation may have been lower and nests were probably available to foxes through 15 to 20 July (see Avian Investigation Section I. Results and Discussion). Although the latest nest on the study plot fledged on 30 July in 1979, the number of nests found by foxes in the study area dropped considerably after the period 6/26 to 7/6 (see Section G. Food Habits). The activity patterns analyzed here were probably strongly affected by stochastic factors, such as weather.

C. Activity budget

Because inactive animals are easier to observe, they were sampled disproportionately. For this reason 84% of the direct observations recorded were of inactive foxes, compared to the more reasonable activity budget estimate of 45% inactive from ground tracking. Because of this difference, activity budget calculations (Table 20) and discussion are based on proportion of hours of observation of active

Table 20. Activity budget of arctic foxes at Demarcation Bay, Alaska in 1979. Data shown in percent of total 1-min interval samples from observation records of active foxes in which each behavior was recorded.

	Tracking periods						
	6/14-25	6/26-7/6	7/7-16	7/17-25	7/26-8/4	8/5-17	Total
Hours of observation of active foxes	14.07	12.32	12.02	12.37	11.47	7.92	70.15
Movements							
Searching	53.85	72.58	42.06	61.03	60.17	56.96	57.69
Slow searching	9.73	9.00	17.41	17.17	13.76	21.73	14.29
Foraging activities							
Pursuit	2.04	2.35	0.42	1.36	1.32	2.74	1.66
Digging	1.56	2.35	0.42	1.23	0.73	0.42	1.18
Eating	1.08	1.66	13.64	3.40	3.80	4.01	4.54
Caching	10.33	1.39	6.82	5.17	1.61	2.32	4.92
Social activities							
Play	0.00	0.69	1.25	0.54	5.42	0.00	1.32
Agonism	3.73	0.41	2.09	0.41	0.00	0.00	1.25
Maintenance activities							
Grooming	3.73	2.22	2.09	1.36	3.81	2.74	2.66

foxes. The total number of hours of observation of active foxes was 70. Based on the estimate of 55% active from ground tracking, Foxes 3 and 5 were observed during approximately 5% of the total hours of activity between 14 June and 17 August.

During 72% of the active time of foxes under observation the animals were engaged in searching. No other single behavior occupied more than 5% of the foxes' activity budgets over the season. Differences in activity budget between 10-d periods are marked in some cases (Table 20). Relatively low values for proportion of hours searching in the period 7/7 to 7/16 are attributable in large part to observations of a pair of foxes utilizing a caribou carcass during several tracking shifts. The importance of slow searching increased somewhat through the season, due perhaps to the decreasing availability of live prey and nests and increasing reliance on caches as a major food source.

Foraging behaviors show seasonal variation. Pursuit behaviors vary primarily due to digging, no other form of pursuit had greater than a few seconds duration. Only pursuit of small mammals involves digging, and, at the densities of small mammals encountered in 1979, digging was rare. All of the variation in the proportion of the activity budget in which foxes were eating is due to consumption of carrion. Foxes used carrion more heavily as the season progressed, the high value in the period 7/7 to 7/16 is attributable to observations made at a single large carcass.

Caching occurred far more frequently in the period of greatest food abundance (6/14 to 6/25) than in any other period. The large amount of time engaged in caching behaviors in the period 7/7 to 7/16 is attributable to a high frequency of caching during active bouts in which foxes consumed large volumes of carrion.

Social activities constituted less than 3% of the activity budget over the season. However, social play bouts in the period 7/26 to 8/4 constituted 5.4% of the 11.5 h of observation of activity. High values for agonism in the periods 6/14 to 6/25 and 7/7 to 7/16 result from different types of agonism. In the period 6/14 to 6/25 a territorial interaction lasting 21 min was observed between Fox 1 and Foxes 5 and 7. In the period 7/7 to 7/16, another territorial interaction between Fox 3 and an unidentified fox lasted 5 min and a high frequency of agonism between Foxes 5 and 7 was observed during feeding bouts at a caribou carcass.

D. Analysis of foraging activities

Continuous data records of all observations of foraging behaviors were used in analysis of foraging activities. The seasonal patterns of foraging and the functional relationship between behaviors were examined.

Captures

Each small mammal, bird, or egg was counted as a separate capture with the exception of longspur nests, which were counted one capture per nest. Captures occurred in every period (Table 21), but at a decreasing

Table 21. Compilation of observations of captures and meals for analysis of foraging behaviors of arctic foxes at Demarcation Bay, Alaska in 1979.

	Tracking periods						
	6/14-25	6/26-7/6	7/7-16	7/17-25	7/26-8/4	8/5-17	Total
Captures[1]							
Total number	57	32	12	21	11	2	135
Captures per hour[2]	4.0	2.6	1.0	1.6	1.0	0.2	1.9
Avian prey	39	20	10	17	8	0	94
Eggs only	38	20	9	11	2	0	80
Chicks only	0	0	0	5	6	0	11
Small mammals	14	10	2	4	2	2	34
Unknown identity	4	2	0	0	1	0	7
Proportion cached	0.63	0.25	0.17	0.48	0.45	0.0	0.45
Meals[3]							
Total number	25	31	25	30	26	24	161
Excluding carrion[4]	25	31	10	25	25	14	130
Avian prey	8	13	4	9	8	2	44
Eggs only	6	10	0	1	4	0	21
Small mammal prey	11	7	2	3	1	1	25
Unidentified	6	11	4	13	16	11	61
Meals per hour[2]	1.8	2.5	2.1	2.4	2.3	3.0	2.3
Excluding carrion[4]	1.8	2.5	0.8	2.0	2.2	1.8	1.8
Meals from caches	5	8	10	15	19	13	70
Proportion from caches[5]	0.20	0.26	1.00	0.60	0.76	0.93	0.54
Caches consumed/hour[2]	0.3	0.6	0.8	1.2	1.7	1.6	1.0

[1] Each small mammal, bird, or egg taken by a fox was counted as one capture, with the of eggs or chicks in longspur nests, which counted as one capture per nest.
[2] Rates computed from min of observation of active foxes only.
[3] A meal of carrion is a single feeding bout. Other food items were counted individually, one meal per small mammal, bird or egg, with the exception of longspur nests, which counted as one meal.
[4] Includes adult birds, chicks and caches of unknown identity.
[5] Proportion of total meals excluding carrion.

rate throughout the summer. The low rate of capture in the period 7/7 to 7/16 is the result of a low number of hours of searching when foxes were feeding on a large carcass during several tracking shifts. The rate of capture was greatest in the first 10-d period, 6/14 to 6/25, the period of greatest food availability. Nearly 70% of all captures in that period were eggs from nests of shorebirds, longspurs, ptarmigan, and waterfowl. Avian nest densities peaked between 10 and 15 June in 1979 (Fig. 12) and bird nests of most common species were essentially unavailable to foxes after mid-July. Fledged chicks were occasionally captured in July and August. Small mammals were captured most frequently in June and early July. Two factors contribute to this distribution of small mammal captures: 1) small mammal numbers appeared to decrease during the summer in 1979, and 2) dispersion of small mammals increased, and their vulnerability to capture by foxes decreased as lemmings moved from "refuge" habitats used during breakup and early summer (see Small Mammal Investigation, II. Discussion). The proportion of captures which were cached rather than consumed is fairly high in every period in which captures occurred. It is greatest in the first 10-d period. The low proportion of captures cached in the period 7/7 to 7/16 is probably related to the low number of captures and low amount of time searching in that period. Over the season approximately 45% of captures observed were cached.

Meals

As with captures, each small mammal, fledged bird, or egg was counted as a single meal, except longspur nests which counted as one

meal per nest. For consumption of carrion a meal is a single feeding bout. In spite of the decrease in rate of capture, the rate of consumption remained remarkably stable (Table 21). Because meals of carrion were of unknown size, and because much of the meat consumed at a carcass was probably regurgitated in caches, meals of carrion are separated from other meals in Table 21. This yields a substantially reduced rate of consumption (relative to other 10-d periods) only in the period 7/7 to 7/16, during which the foxes under observation consumed large amounts of carrion and spent little time searching for other food. The proportion of meals from caches shows an increase through the summer, with the exception again of the period 7/7 to 7/16. Many of the unidentified meals were from caches. The data indicate that the rate of consumption remained remarkably stable through utilization of caches.

Caching

Caching is a strategy to regulate food availability during fluctuations in prey availability, and it apparently provided sufficient food resources for the foxes to maintain a constant rate of intake of food over the period of observation. Caching occurred during every 10-d period (Table 22), but was much more frequent in the period 6/14 to 6/25, in which nests of sandpipers and longspurs were most abundant. A high rate of caching also occurred in the period 7/7 to 7/16; most of these caches were of caribou meat from a carcass. Eggs were cached much more frequently than other food items; 60% of the eggs taken from nests were cached, compared to only 27% of the small mammals captured and 9% of the fledged birds.

Table 22. Compilation of observations of caches for analysis of foraging behaviors of arctic foxes at Demarcation Bay, Alaska in 1979.

	Tracking periods						
	6/14-25	6/26-7/6	7/7-16	7/17-25	7/26-8/4	8/5-17	Total
Caches							
Total number[1]	36	8	25	12	11	7	99
Excluding carrion	36	8	10	11	11	4	80
Caches per hour[2]	2.6	0.6	2.1	1.0	1.0	0.9	1.4
New caches per hour[3]	2.5	0.6	1.4	0.9	0.4	0.4	1.3
Caches of eggs	30	5	7	4	1	0	47
Caches of carrion	0	0	15	1	0	3	19
Caches of small mammals	3	2	0	2	1	1	9
Other caches[4]	3	1	3	5	9	3	24
Caches found	5	8	18	16	25	17	89
Caches found per hour	0.3	0.6	1.5	1.3	2.2	2.1	1.3
Recaches	0	0	8	1	6	4	19
Rate of cache accumulation[5]	+2.2	+0.0	+0.6	-0.3	-1.3	-1.2	+0.0
Cumulative no. of caches minus cumulative no. of caches used[1]	31	31	46	43	35	29	

[1] Including recaches.
[2] Rates computed from min of observation of active foxes only.
[3] Excluding recaches.
[4] Includes adult birds, chicks and caches of unknown identity.
[5] The rate of cache accumulation is the number of new caches per h minus the number of caches used per h.

Caches were discovered by foxes at an increasing rate through the summer. Two factors contribute to the increasing rate of cache discovery: 1) cache density increased at least through the period 7/7 to 7/16, as indicated by the rate of cache accumulation; and 2) decreasing availability of prey made more of the activity budget available to locate caches. In the period prior to 7 July, when fresh prey was most available, foxes consumed all caches discovered. In other periods, in which larger numbers of caches were found, many food items taken from caches were not consumed but were recached 50 to 100 m from their original location. A fresh cache may be more easily located than an old cache. The habits of moving caches and utilizing caches when fresh prey are available increased the ratio of new to old caches and may have increased the fox's efficiency in locating caches.

The rate of cache accumulation indicates that there was no net accumulation of caches over the season. However, a large number of caches were still available. Assuming that most recaches were previously unrecorded, the cumulative number of caches minus the cumulative number of caches used (Table 22 and Fig. 15) indicates that 30% of the known cached food supply remained. The rate of depletion of the known cached food supply (Fig. 15) indicates that the ability of the foxes to locate cached food had not decreased by 17 August. The estimate that 70% of the cached food supply had been utilized prior to 17 August is a maximum estimate. Observations of foxes began on 14 June. The average date of nest initiation in 1979 was 6 June and the number of nests active peaked around 12 June. Small mammals were more

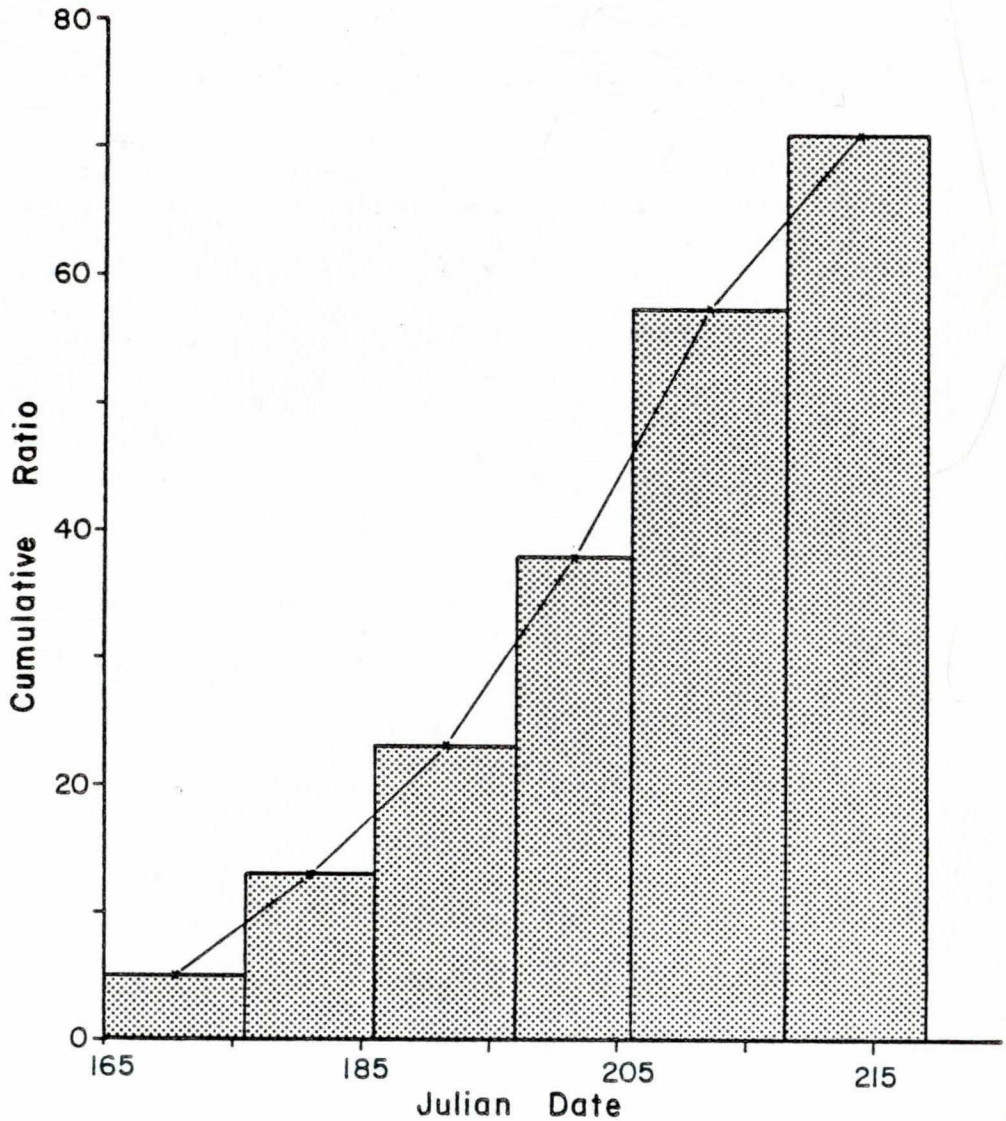

Figure 15. Cache utilization by arctic foxes at Demarcation Bay, Alaska in 1979. The value of the y-axis in any period is the cumulative proportion of the season's total observed cached food supply used. The slope of the line is an estimate of the rate of depletion of the total known cached food supply.

available when concentrated in refuge habitats between approximately 30 May and 29 June. Considering the high rate of caching in the first period of observation, much of the cached food supply may have been stored prior to initiation of observations. The foxes under observation were successful in regulating food availability through use of dispersed caches at least through 17 August.

Scent-marking

Arctic foxes were observed scent-marking (urinating) 1328 times. The average interval between consecutive scent-marks was 1.62 min (n=1066 intervals). The rate of scent-marking was calculated as 18.9 scent-marks per h of activity (Table 23). The 2 female foxes (numbers 3 and 5) show dissimilarities in both average rate of marking and in seasonal trends (Table 23). Fox 3 maintained a relatively high and stable rate of marking averaging 29.2 marks/h. Female 5 showed a lower average marking rate (14.9 marks/h) and the rates decreased substantially in nearly every 10-d period. This may be related to age differences, or some other factor, or simply reflect individual variation. Observations of male foxes were infrequent and of short duration. In addition, males were observed most frequently when in the company or vicinity of their mates. These factors may account for the low estimated rates of scent-marking for males (Table 23).

The high rates of urination and its characteristic odor are indications that such scent-marking possesses social or ecological significance. In red foxes, scent-marking may serve social functions in both territory or "social record" marking (Tinbergen 1965, Fox 1971),

Table 23. Compilation of observations of scent-marks of arctic foxes at Demarcation Bay, Alaska in 1979. Rates are calculated per hour of observation of active foxes.

	Tracking periods						
	6/14-25	6/26-7/6	7/7-16	7/17-25	7/26-8/4	8/5-17	Total
Total scent-marks	322	319	229	222	124	112	1328
Scent-marks/h	22.89	25.90	19.06	17.95	10.81	14.15	18.93
Fox 3							
Total marks	90	172	118	108	37	107	632
Scent-marks/h	26.73	39.54	31.33	25.41	25.52	23.78	29.15
Fox 5							
Total marks	207	112	106	112	85	5	627
Scent-marks/h	22.22	18.82	15.55	14.80	9.36	1.50	14.90
Females							
Scent-marks/h	23.42	27.57	21.16	18.62	11.58	14.30	19.75
Males							
Total marks	10	32	5	2	2	0	51
Scent-marks/h	8.33	18.29	3.95	3.64	2.14	0	8.82

and in pair-formation and behavioral preparation for mating (Macdonald 1979, Henry 1980). Some red fox scent-marks also serve non-social, foraging purposes (Henry 1977). Scent-marks of arctic foxes during this study were examined for relationships with other foraging behaviors. No data are available from the mating season and nearly all data are from female arctic foxes. Social functions of scent-marks are treated in Section E (Analysis of Social Activities).

Four foraging behaviors were examined for a relationship with scent-marking: caches, captures, meals, and cache retrievals. However, while scent-marking occurred at regular intervals throughout fox activity periods, other foraging behaviors occurred less regularly as food items were encountered. For this reason, only a small number of scent-marks occurred in association with recognizable foraging behaviors (although "searching" obviously serves foraging functions, the foxes' motives are not explicit). In addition, certain foraging behaviors tend to be exhibited in repeated sequences. This lack of independence causes the rate of scent-marking to decrease when foraging behaviors are being exhibited (Table 24) but this does not indicate a negative relationship between scent-marking and foraging activities.

Intervals between scent-marks associated with captures were shorter than intervals between scent-marks associated with other foraging behaviors (Table 24). The interval between scent-marks associated with each foraging behavior decreased in the following order: captures, meals, caches, cache retrievals. Because several foraging behaviors occur in sequences, they are not independent events; therefore only 2

Table 24. Intervals between scent-marks (min) of arctic foxes at Demarcation Bay, Alaska in 1979.

	N	Average (min)	SD
Interval between all consecutive scent-marks	1066	1.62	2.28
Interval between scent-marks before and after a cache	68	4.50	3.42
Interval between scent-marks before and after a capture	41	3.96	2.82
Interval between scent-marks before and after retrieval of a cache	40	5.46	6.24
Interval between scent-marks before and after a meal	54	4.20	4.38

foraging behaviors were tested for equal intervals between associated scent-marks. A capture and a cache retrieval are independent events; they also show the greatest and the least association to scent-marks by this analysis. However, no significant differences were found in mean length of intervals between scent-marks ($p>0.05$).

The distribution of scent-marks in 15-s intervals for 5 min before and 5 min following each of the 4 foraging behaviors was also examined (Fig. 16). The distributions of scent-marks around 2 foraging behaviors, caches and captures, were found to differ significantly from a uniform distribution calculated for 15-s intervals (χ^2, $p<0.05$). The numbers of scent-marks in 15-s intervals around cache retrievals and meals did not differ from the uniform distribution. Expected values for a uniform distribution were calculated by multiplying the rate of scent-marking per 15-s interval (0.0789, calculated from Table 23) by the number of observations of the foraging behavior being tested. Observations of foraging behaviors which were not followed or preceded by 5 min of direct observation were excluded from the analysis. The significance values of the chi square statistic are inflated by low expected values (between 3.5 and 4.7 for all tests), the result of low number of observations of foraging behaviors. This increases the probability of identifying a significant variation from a uniform distribution in a truly uniform data set. Because of lack of independence between various foraging behaviors and interference between behaviors (i.e. only one behavior can be exhibited at any moment) the actual distribution of scent-marks is unlikely to be strictly uniform in

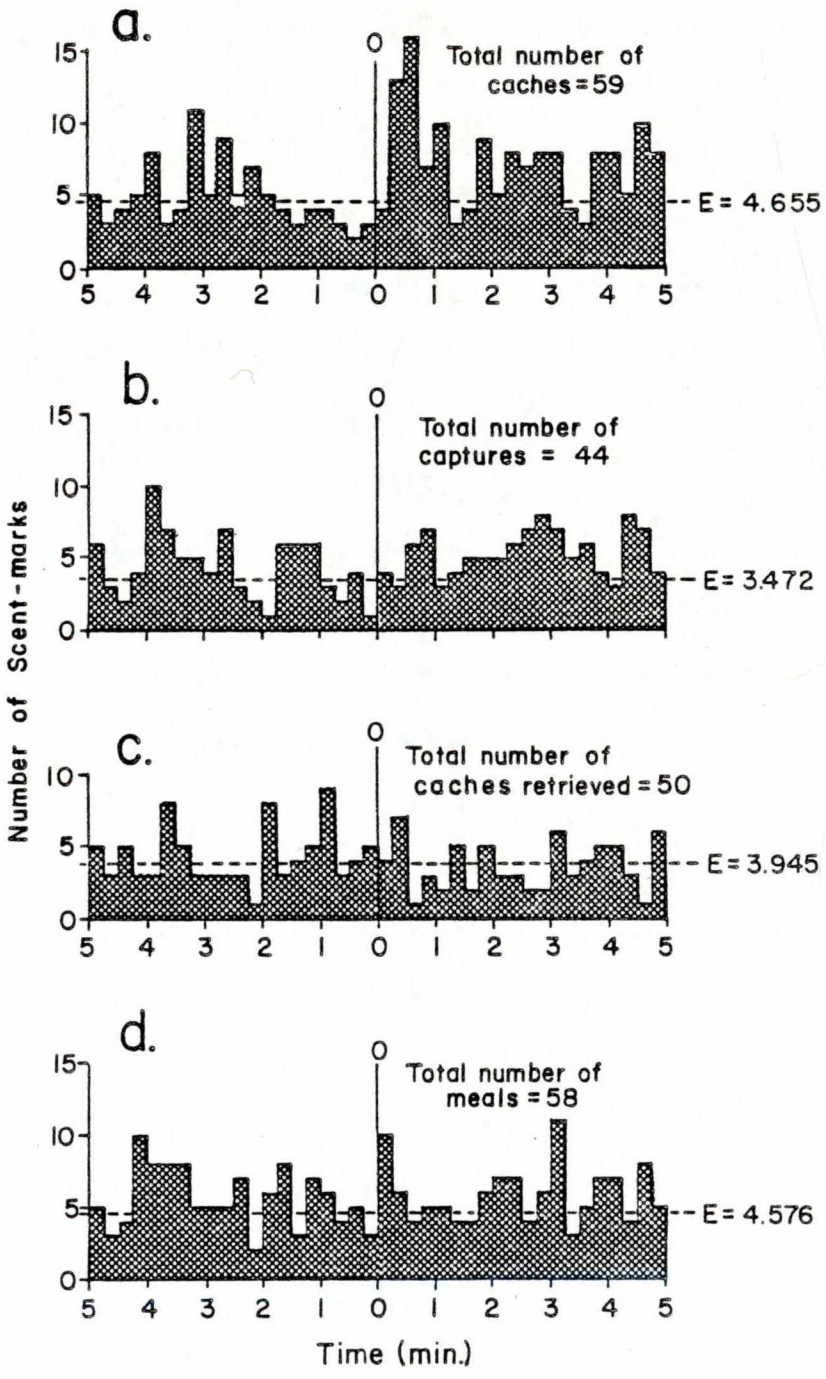

Figure 16. Number of scent-marks of arctic foxes observed at Demarcation Bay, Alaska in each 15-s interval for 5 min before and 5 min after 4 foraging behaviors in 1979: a) caches, b) captures, c) cache retrievals, and d) meals. The foraging behavior in each histogram occurs at time 0. E is the value expected assuming a uniform distribution of scent-marks/15-sec interval (see text).

the vicinity of any foraging behavior. The larger-than-average interval between scent-marks associated with foraging behaviors (discussed above and in Table 24) is reflected in the low observed values for the number of scent marks in the 15 s intervals prior to some foraging behaviors (Fig. 16). For example, it is clear that during the period immediately prior to a cache the fox was engaged in activities which precluded or reduced the frequency of scent-marking. Nonetheless, the distributions of scent-marks around meals and around cache retrievals were not found to differ significantly from the uniform distribution.

The distribution of scent-marks in 15-s intervals around a cache peaks between 15 s and 75 s following the cache (Fig. 16). There are few scent-marks between 1.5 min before and 15 s after the cache, when the fox is finding, carrying, and caching the item. The distribution of scent-marks before a capture shows a similar decrease immediately prior to capture, perhaps during slow searching or pursuit. A peak in marking frequency occurs approximately 3 min after a capture; however, observed values are larger than expected from 1.5 min to 3.75 min following a capture. This delayed peak probably indicates that many of the scent-marks occurring within 5 min after a capture are associated with a subsequent cache of the food item. Approximately 50% of all captures made were subsequently cached (Table 21).

In conclusion, some scent-marks appeared to occur in conjunction with caches and captures, but rarely was there a relationship between scent-marks and meals or cache retrievals. Scent-marks appeared to have been only secondarily related to some captures. Instead they were

primarily related to a subsequent cache of the food item. The association of scent-marks with caches leads to the conclusion that scent-marks denote the location of utilizable food, rather than the lack of food at a previously searched site, as Henry (1977) suggested for red foxes. However, it should also be mentioned that only a very small proportion of scent-marks observed could be related to one of the 4 foraging behaviors. Therefore, additional functions must be hypothesized. In addition, although some scent-marks appeared to be related to caches, foxes were never observed to scent-mark directly on the cache site. Foxes were rarely seen to scent-mark directly into a plundered nest, but failed nests on the 30-ha study plot were often found torn apart and/or with fox odor from urine, or fox feces in the nests. On several occasions the nest bowl was torn apart and scent was deposited several hours or days after the eggs disappeared. These observations are difficult to interpret and the intended functions of different scent-marks remains illusory. Obviously, a scent-mark may serve several functions depending on the circumstances, including unmeasured characteristics of the site which may have stimulated marking. Any single mark may also serve more than one function when perceived by a conspecific.

E. Analysis of social activities

Intraspecific agonism

Observation of intraspecific agonism could be divided into 2 categories: agonism between members of a mated pair and territorial

interactions. Neither type of agonism occurred frequently, so most discussion is descriptive and qualitative. The total amount of time foxes were observed in agonistic behavior was very small, 0.44 h or 1.25% of the activity budget (Table 20).

Seventeen instances of agonism between 2 foxes were recorded, all between 21 June and 28 July. Thirteen of these were between members of a mated pair; only 4 were territorial interactions between residents and interlopers.

Four territorial agonistic interactions between foxes lasted between 30 s and 21 min. The longest interaction occurred on 21 June and involved 3 foxes, beginning when Fox 5 was chased by Fox 1. The interaction may have been prolonged by the lameness of Fox 1. Fox 5 retreated to a gravel spit in the bay where her uncollared mate was sleeping. Here Fox 1 turned to retreat from Fox 7 (the mate of Fox 5). When Fox 1 entered the shore-fast ice off of Demarcation Point, Fox 7 stopped pursuit.

Although scent-marks are generally ascribed social functions related to territorial marking, or social record, such a function is difficult to demonstrate. Scent-marks may indeed have an agonistic function between resident foxes and interlopers in a defended territory. However, on the single occasion in which observations of a fox were made for 5 min following an episode of territorial aggression, the aggressive fox (a female) scent-marked 7 times in the 5 min, which is slightly less than the expected rate (8.1/5 min).

Non-agonistic social interactions and play

Non-agonistic social interactions occurred only between members of a mated pair. Any sighting of 2 foxes within several hundred meters of one another and apparently aware of one another was counted as a non-agonistic interaction. Non-agonistic interactions also included observations of 2 foxes sleeping within 50 m of one another. These were the longest "interactions" of this type, up to 6 h, and occurred only at mid-day. Arctic foxes were never observed to rest or sleep in direct contact, but frequently within several meters. Instances of non-agonistic interactions were definitely underestimated because of our dependence on an auditory clue or a direct sighting of the male fox. Of 30 such interactions between active foxes, 16 were accompanied by vocalizations of one or both foxes. Again, this is an underestimate because of our inability to perceive vocalizations. On several occasions foxes were in proximity for extended periods without discernible auditory or behavioral communication. Vocalizations of a mate were frequently unanswered by the fox under observation and often elicited no discernible behavioral response. We were unable to monitor the male foxes and were therefore unaware of their movements prior to sighting or for a long period subsequent to sighting. Frequently the male would be resighted several times over a 3- to 9-min period of observation of the female. For this reason I have assigned a minimum duration of 5 min to these types of non-agonistic social interactions.

Table 25 summarizes observations of non-agonistic social interactions. Over the entire season, members of a mated pair were

Table 25. Seasonal distribution of hours of non-agonistic social interactions and play for 2 arctic fox pairs at Demarcation Bay, Alaska in 1979.

	Tracking periods						
	6/14-25	6/26-7/6	7/7-16	7/17/25	7/26-8/4	8/5-17	Total
Foxes 1 and 3							
Hours of interaction	8.27	0.38	0.33	0.26	0.83	0	10.07
Proportion of hours of observation	0.53	0.02	0.02	0.02	0.04	0	0.10
Hours of play	0.003	0.003	0.051	0	0.736	0	0.793
Proportion of hours of observation	0.0002	0.0002	0.0031	0	0.0400	0	0.0082
Foxes 5 and 7							
Hours of interaction	0	0.28	5.52	0.28	0.08	0.09	6.25
Proportion of hours of observation	0	0.03	0.41	0.02	0.01	0.01	0.083
Hours of play	0	0.001	0.001	0.077	0	0	0.0790
Proportion of hours of observation	0	0.0001	0.0001	0.0046	0	0	0.0010
Total for all foxes							
Hours of interaction	8.27	0.67	5.85	0.55	0.92	0.09	16.35
Proportion of hours of observation	0.23	0.02	0.19	0.02	0.03	0.003	0.095
Hours of play	0.003	0.004	0.052	0.077	0.736	0	0.8720
Proportions of hours of observation	0.0001	0.0001	0.0017	0.0023	0.0255	0	0.0050

observed together (i.e. within several hundred meters of one another) about 10% of the time. Mated pairs seemed to be together most during the periods 6/14 to 6/25 and 7/7 to 7/16, but this was due primarily to observations of pairs sleeping together in the first period and from observations of sleeping and communal use of a caribou carcass in the second.

Play behaviors were more easily discerned than non-agonistic social interactions as foxes were in direct contact or very close. Eleven occurrences were observed ranging in duration from several seconds to 24 min. Play postures were often assumed by one fox without a response from the other fox. Only 2 bouts were of greater than 3 min duration; they were 20 min and 24 min long and occurred on 27 and 28 July between Fox 5 and her mate. An analysis of seasonal trends is not possible because play was so rarely observed. However, play did occur as late as 28 July, long after the potential reproductive season had ceased. Overall, foxes were observed playing in only 0.5% of total observations.

F. Habitat use

Foxes rested in dry areas in any vegetation type, but some areas were used regularly. The 3 most frequently used areas for resting were: 1) an area in dry coastal polygons with very deep troughs and ice-wedge caves used by Foxes 1 and 3; 2) a rich Dupontia meadow with remains of an old cabin used by both pairs of foxes (at different times); and 3) a small inactive den located in high relief lcp which was used by Fox 5 and her mate. The use of these areas was variable and inconsistent and

none formed a center of activity. When a fox was in the vicinity of one of these areas in late morning it would rest there; if not, another site was used. Foxes were never observed to "travel" in a straight line to a resting area.

Data on habitat use of active foxes are presented in Table 26. Preference ratios (PR) for each habitat were calculated from the following formula:

$$PR = \frac{M_i}{\sum_{i=1}^{n} M_i} \cdot \left[\frac{N_i}{\sum_{i=1}^{n} N_i} \right]^{-1}$$

where M_i is the number of minutes of observation of the fox in vegetation type i; N_i is the areal extent (km^2) of vegetation type i in the foxes' home range (Table 27); and n is the total number of vegetation types in the foxes' home range.

The habitat use patterns of Foxes 3 and 5 were quite similar, differences which occurred were in rare vegetation types and due primarily to differences in extent of those types in each foxes' home range (Table 27). In general, the most used vegetation types, medium relief lcp and meadow, were the most widely available and these were used in proportion to their occurrence in the foxes' home ranges. The only other extensive vegetation type, low relief lcp, appeared to be selected against. The less common vegetation types were all used in greater proportion than availability with the exception of tussock slope which was consistently selected against (PR=0.24). Gravel beaches were

Table 26. Habitat use of active arctic foxes at Demarcation Bay, Alaska in 1979. Codes are as defined in Table 1.

	Vegetation types											
	M	LR	MR	HR	TS	HCP	GB	DCP	SB	CP	W	Total
All foxes combined												
Min observation	963	423	1538	438	124	241	217	386	1	66	22	4419
Preference ratio	1.25	0.58	0.97	5.82	0.23	2.35	7.00	3.48	0.10	3.75	0.05	-
6/14-25	0.62	1.08	0.82	11.59	0.20	2.39	7.14	2.72	0	1.25	0.22	-
6/26-7/6	1.44	0.31	0.72	9.06	0.36	2.83	3.57	4.32	0	11.50	0	-
7/7-16	0.85	0.08	1.85	2.65	0.14	1.43	4.57	1.36	0	1.75	0	-
7/17-25	1.43	0.61	0.72	4.47	0.26	3.04	9.57	4.80	0	7.50	0	-
7/26-8/4	1.89	1.02	0.96	2.23	0.15	2.83	3.57	0.44	0	0	0	-
8/5-17	1.46	0.19	0.68	3.47	0.28	1.35	16.14	9.04	1.00	0	0.04	-
Number of captures:												
Avian	23	10	44	5	2	3	0	4	0	1	0	92
Mammalian	4	5	13	6	0	2	0	3	0	0	0	33
Total	29	16	59	12	2	5	0	7	0	1	0	131
Captures/hour	1.8	2.3	2.3	1.6	1.0	1.0	-	1.1	-	0.9	-	1.8
Scent-marks	247	153	493	135	15	64	59	102	0	33	0	1301
Scent-marks/hour	15.4	21.7	19.2	18.5	7.3	16.0	16.3	15.8	-	30.0	0	17.6
Number of caches	9	10	56	5	1	7	1	6	0	1	0	96
Caches/hour	0.5	1.4	2.2	0.7	0.5	1.7	0.3	0.9	-	0.9	-	1.3
Fox 3												
Min observation	289	41	424	74	66	88	128	230	0	34	0	1374
Preference ratio	1.09	0.16	0.91	3.86	0.56	12.80	15.50	5.57	0	5.00	0	-
Fox 5												
Min observation	604	348	989	327	52	137	43	133	1	11	7	2652
Preference ratio	1.25	0.70	1.08	4.92	0.14	1.16	16.00	4.17	0.13	1.33	0.05	-

Table 27. Vegetation type distributions in the home ranges of 2 female foxes at Demarcation Bay, Alaska in 1979. Codes are as defined in Table 1.

	Total Study Area		Home Range Fox 3		Home Range Fox 5		Area of
	Area(km^2)	Prop.	Area	Prop.	Area	Prop.	Overlap
M	6.42	0.17	4.61	0.19	3.37	0.18	1.55
LR	6.09	0.16	4.48	0.19	3.44	0.19	1.81
MR	13.29	0.36	8.05	0.34	6.37	0.34	1.61
HR	0.62	0.02	0.36	0.01	0.47	0.02	0.23
TS	4.40	0.12	2.05	0.08	2.64	0.14	0.52
HCP	0.85	0.02	0.13	<0.01	0.83	0.04	0.13
GB	0.26	0.01	0.15	0.01	<0.01	<0.01	-
DCP	0.93	0.02	0.72	0.03	0.23	0.01	0.10
SB	0.05	<0.01	-	-	0.05	<0.01	-
CP	0.15	<0.01	0.13	<0.01	0.05	<0.01	0.03
Water/ice	3.91	0.11	3.29	0.14	1.09	0.06	0.41
Total	36.97		23.97		18.54		6.39

used in much greater proportion than availability (PR=12.2). High relief high center polygons were also highly selected for (PR=5.8).

Disturbed vegetation types cannot be given preference ratios because of their extremely low availability. However, the dozer trail was most definitely a preferred use area which foxes used during 95 of the 4517 total min of observation. Four captures were observed there.

No distinct seasonal trends in habitat use are evident from Table 26, with the possible exceptions of a decreasing use of high relief lcp and a decrease from a peak of use between 6/26 and 7/6 of coastal ponds. However, the total number of minutes of observation per period is small, especially considering the low availability of these vegetation types.

The highest rates of capture and the largest number of captures of prey items occurred in the 3 most extensive vegetation types: low relief lcp, medium relief lcp, and meadow. High relief lcp supported a similarly high rate of capture. Gravel beaches, with the highest preference ratio, supported no captures and few meals. The preference for beaches may have been due in part to opportunistic location of carrion (one fox was observed discovering a seal carcass on the beach). It may also be preferred because it is an easily traversed terrain. Beaches were used as play areas when unusual items or redolent substances were found. Foxes thoroughly investigated and frequently rolled in putrifying items found on the beach.

Fourteen of 29 captures in meadows occurred on pond shores and all of these were avian prey, predominantly eggs. The rate of capture in

each vegetation type, excluding gravel beaches, varied from 0.9/h to 2.3/h, which indicates that the foxes were able to capture prey with roughly equal efficiency in each vegetation type. Seasonal trends in capture rates were similar for both small mammal and avian prey; and all vegetation types showed a decreasing rate of capture throughout the summer. The largest number of captures of both small mammal and avian prey occurred in medium relief lcp. The next highest number of captures of avian prey occurred in meadows; for small mammal prey the next highest number occurred in high relief lcp.

Vegetation types which supported high rates of capture also had high rates of scent-marking. Gravel beaches were the only vegetation type in which low rates of capture were observed in conjunction with high rates of scent-marking. Beaches were used as highways by non-resident foxes and many observations of unrecognized foxes occurred on beaches. The presence of sign of non-resident foxes may have been a stimulus for an increased rate of scent-marking on beaches by territorial residents. The parallel between scent-marking rate and capture rate in each vegetation type may indicate that foxes are more territorial in areas with higher prey densities, or that scent-marking serves some function in foraging in addition to territorial marking, as suggested in Section D (Analysis of Foraging Behaviors).

G. Food habits

Data on meals are presented in Table 21. Many food items were unidentified, particularly when foxes fed from caches. Birds of all

species were nearly always attracted to a fox and were more active and conspicuous when a fox was near, making identification of nests taken by the fox difficult. Nests found by foxes were often identifiable to species for shorebirds and ptarmigan, but predation of longspur nests was very quick and identified only by observation of the escaping female. Therefore, estimates of the frequency of longspur nests in the diet are probably low (see also Avian Investigation, Section I. Results and Discussion). Even with shorebirds, mobbing and calling by several birds of different species frequently made identification of the nest impossible. Foxes were observed to take eggs and chicks of semipalmated sandpipers, red-necked phalaropes, stilt sandpipers, arctic loons and Lapland longspurs. Captures of small mammals were easily identified by the foxes' behavior prior to capture and the relatively prolonged handling time, though the species of small mammal was rarely determinable.

Although 38% of the meals in Table 21 are unidentified (most of these are from caches), avian prey appear to be the single most important food source. Eggs comprised 85% of the avian prey captured, and chicks comprised another 12%; the remainder were adults or fledglings captured by stalking (2 longspurs and one small sandpiper, probably semipalmated). The proportion of eggs found which were subsequently cached was 58.8%; only 27.3% and 9.1% of the small mammals and fledged birds captured were cached. The fact that captures of small mammal prey were unlikely to be unidentified supports the contention

that small mammals comprised a small proportion of the unidentified meals.

The relative importance of carrion in the diet of these foxes in 1979 is difficult to assess. While the quantity of food consumed in a "meal" of avian or small mammal prey varies somewhat, the quantity of digestible meat consumed per "meal" at a carcass can vary tremendously. Caribou formed by far the largest proportion of carrion in the diet, which also included seal and various large birds. Nearly 20% of the known cached food supply was carrion and these caches may have formed a relatively large proportion of the unidentified meals.

In summary, the data show: 1) a heavy reliance on avian prey, particularly eggs, both during the nesting season and afterwards from cached sources; 2) a sharp decrease in the number of meals of small mammals after 6 July; and 3) a decline in availability of all food types except carrion through the summer, accompanied by increased reliance on cached foods and carrion.

H. Home range and movements

The distance moved during a tracking period depends on the activities of the fox. The total distance moved in a tracking period varied from 0 km (6.5-h tracking period) to 29 km (7.6-h tracking period). In each 10-d period, foxes were tracked between 45.9 and 93.1 km (Table 28). The total tracking distance was 369.9 km. Average rates of movement per 10-d period show no seasonal trends (Table 28).

Table 28. Average rate of movement (km/h) of arctic foxes and distance moved (km) during activity bouts in each observation period at Demarcation Bay, Alaska in 1979.

Observation Period	Fox 3		Fox 5		Foxes combined	
	rate	distance	rate	distance	rate	distance
6/14-25	2.24	16.4	2.45	40.2	2.39	56.6
6/26-7/6	3.48	33.4	2.47	31.0	2.91	64.4
7/7-16	3.80	41.8	0.96	11.0	2.36	52.8
7/17-25	3.40	28.2	3.32	64.9	3.35	93.1
7/26-8/4	3.02	19.1	2.45	38.0	2.62	57.1
8/5-17	3.47	33.7	2.57	12.2	2.50	45.9
Total	3.31	172.6	2.46	197.3	2.72	369.9

Home ranges for female Foxes 3 and 5 were estimated by the area enclosed in a convex polygon formed by connecting the farthest observed locations (Fig. 17). No analysis of seasonal change in home range size or use areas can be made with the low number of hours of tracking per period. The home range size of Fox 5 did not increase after the period 7/17 to 7/25, suggesting that the observations were sufficient for an accurate estimate of home range size. This method gives a minimum estimate of home range size of 23.9 km^2 (20.7 km^2 dry land) for Fox 3 and 18.5 km^2 (17.4 km^2 dry land) for Fox 5. The home ranges of the 2 female foxes overlapped considerably, the shared area being 6.0 km^2. The overlap area of the home ranges of these females was frequently traversed by both foxes, and several encounters between foxes were observed.

These home ranges are large, but within the range reported for arctic foxes. Estimates of home range size based on direct observation in other studies are: 20.8 km^2 (SD=12.5, n=4; 10.4 km^2 dry land) at Prudhoe Bay (Eberhardt et al. 1982), and 2.9 km^2 (dry land only, n=4) (Speller 1972). Skrobov (1968, from Speller 1972) indicates that home range sizes may vary by a factor of 6, depending on food abundance. Shibanoff (1958) found that the daily range of arctic foxes in the denning season depended on the availability of food. Speller (1972) also found breeding arctic foxes to move greater distances from dens in periods of low lemming availability.

It is difficult, on the basis of information given, to determine relative prey densities under which other reported home ranges were

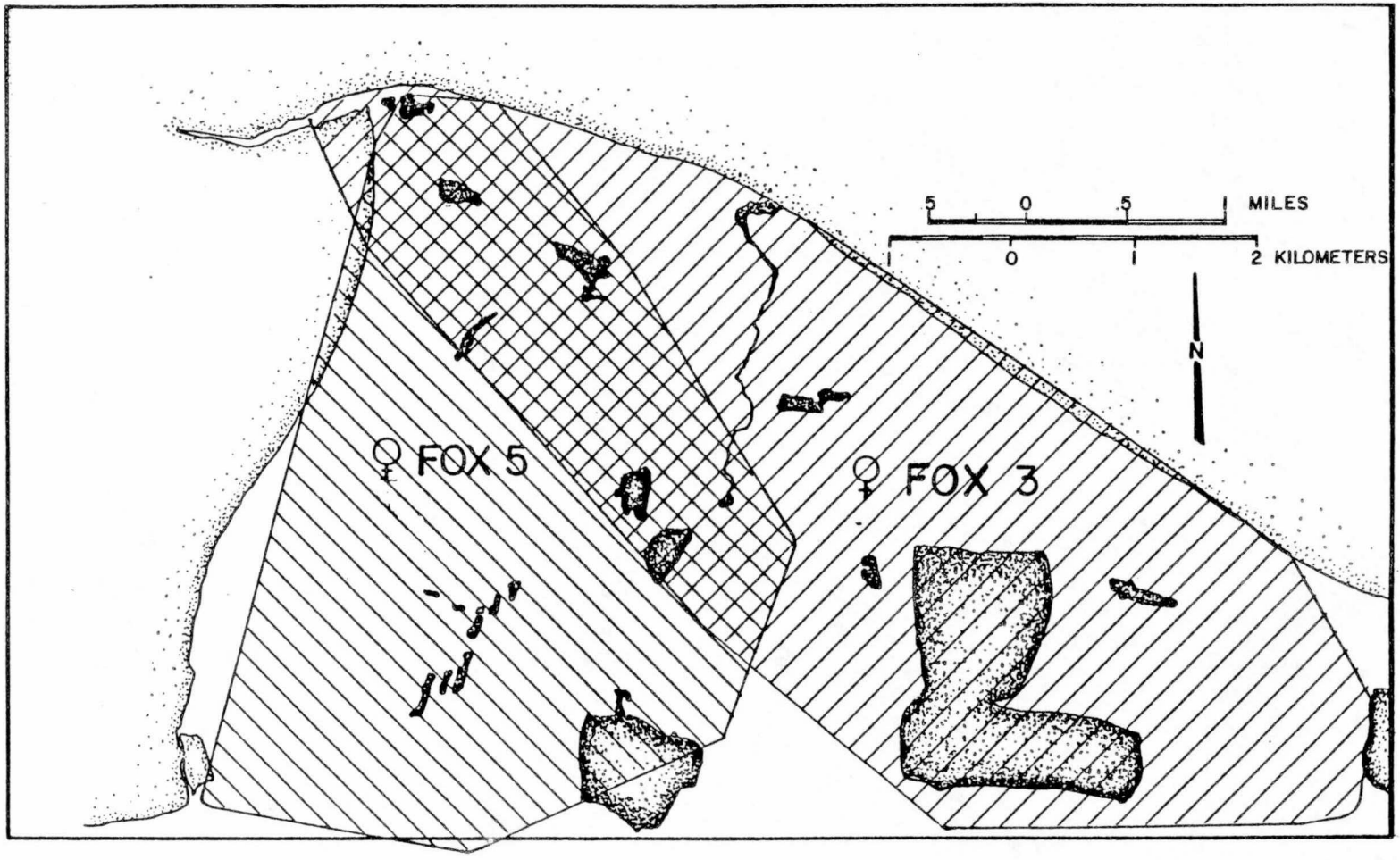

Figure 17. Map of home ranges for two female arctic foxes at Demarcation Bay, Alaska in 1979.

measured. Although Eberhardt et al. (1982) studied foxes both with and without dens, the status of the 4 foxes for which home range could be measured is not given. The large dry-land home ranges observed here, in spite of the lower food requirements due to failure to breed, are not surprising considering the very low levels of food availability. The fact that foxes remained territorial and non-migratory over this season indicates that they maintained foraging efficiency by caching food throughout a familiar home range, which thus provided a constant intake of food over the season at maintenance level or better.

It is not known how late into the fall or winter Foxes 3 and 5 maintained their home ranges. The initiation of fall movements in arctic foxes has been attributed to food scarcity (Chesemore 1967) and the availability of cached food was declining. Through 17 August Foxes 3 and 5 (and their mates) had succeeded in regulating food availability, but they may have been approaching the point of decreasing returns in the maintenance of their ranges and would therefore soon disperse or greatly increase their movements in search of food.

CONCLUSIONS

This investigation examined the summer ecology and behavior of arctic foxes during a period of low small mammal availability accompanied by lack of pup production. The arctic foxes studied remained mated throughout the summer and defended large territories from neighboring animals. Although play was occasionally observed between members of a mated pair, most interactions demonstrated a tolerance of the mate rather than a highly social relationship. When feeding at a carcass, members of a mated pair were intolerant of one another.

The lack of reproduction may have been the result of low availability of small mammal prey. This is supported by the capture data for small mammals. Population size and demography of Lemmus were quite different in 1978 when one active den was located in the study area. Although study area densities of small mammals were not particularly high in either year, the 1979 densities were consistently only 12 to 24% of those for 1978. The age/weight distributions and productivity were also different between years. The 1978 data indicated a productive and stable or increasing L. sibericus population, while in 1979 the parameters were typical of a declining population.

Nest densities of birds were similar in 1978 and 1979. However, the availability of eggs to foxes was quite different due to a dramatic change in phenology of nesting. The difference between years can be attributed to weather events in 1978 causing late and asynchronous nest initiation and nest failure for some species.

Data on nest predation also indicate a difference in behavior and food habits of arctic foxes between years. Predation was high in 1979 and nest losses were safely attributed to foxes. Lapland longspurs appeared to be particularly susceptible to fox predation, suffering 100% nest loss on the study plot in 1979. In 1978, few nests were taken by foxes on the 30-ha study plot and most instances of nest predation were attributed to jaegers.

The adaptiveness of defense of resources and low tolerance for competitors is demonstrated by the data on caching and cache utilization. During periods of overabundance of utilizable resources, foxes cached more food than they ate. When nests were no longer available, the same rate of consumption of food was maintained through feeding almost entirely from caches. In this study, it appeared the foxes had utilized a maximum of approximately 70% of the cached food supply by mid-August and that their efficiency in locating caches had not declined considerably by that time.

That activity bout durations showed no trends paralleling prey availability further supports the contention that foxes were able to regulate their food supply during a season of fluctuating prey availability. Activity bout durations were affected mostly by weather, with foxes resting longer and more frequently during wet weather.

Scent-marking in foxes has been found to serve many purposes, including territory defense, social record, mate-seeking, and increasing foraging efficiency. Some scent-marks observed in this investigation appeared related to captures and/or caches and these scent-marks

probably facilitated regulation of food availability through caching. No relationship of scent-marks was found with either cache retrieval or consumption of a meal. In addition, the primary aim of some scent-marks and the secondary effect of all scent-marks may have been to facilitate the defense of a discrete and regulated resource during the summer period.

The rate of scent-marking declined substantially over the summer for 1 female fox while the other female maintained a relatively constant and consistently higher rate. In general, rates of scent-marking paralleled rates of capture in all vegetation types but gravel beaches, where high rates of marking accompanied the lowest rates of capture. This and the fact that most scent-marks could not be attributed a function or a relationship to any other behavior indicates that many scent-marks serve additional functions unrelated to foraging.

At the levels of prey abundance observed in this study, the most used vegetation types were the most widespread. Of the most used vegetation types, only low relief lcp and tussock slope appeared to be used less than expected based on their distribution. Uncommon vegetation types were all used more than expected, but the major portion of the foxes' time was spent in the 2 most widespread vegetation types: medium relief lcp and meadow.

L. sibericus, the preferred prey, was most abundant in medium relief lcp and more small mammal captures by foxes occurred there than in any other type. Estimates of nest densities of birds were highest in tussock slope, low relief lcp and meadow; high center polygons and

medium relief lcp had lower densities and few birds nested in the rare vegetation types. However, the data on vegetation type preferences of birds are limited and the largest number of nest "captures" by foxes occurred in medium relief lcp. Total rates of capture of both avian and mammal prey were highest in medium relief lcp (1/26 min), low relief lcp (1/26 min) and meadow (1/33 min).

Avian prey was found to contribute more to the foxes' diets than small mammal prey at the levels of availability during this study. The relative importance of carrion is difficult to assess, particularly because food items taken from caches were usually impossible to identify. When few nests were available in late summer foxes relied heavily on food from cached sources. Foxes cached approximately 60% of the eggs found and about 30% of the small mammals captured. Cached food formed 44% of the foxes' diets throughout the summer, and up to 73% in some 10-d periods.

Home ranges of 2 female arctic foxes were 18 and 24 km^2 with approximately 6 km^2 overlap. The depletion of caches below some density would presumably cause the foxes to abandon defense of their home ranges, and switch to the wandering or migratory behavior typical of arctic foxes in late fall and winter. Although the results indicated that cache density was decreasing after 17 July, few of the observations seemed to indicate changes in behavior or movements indicative of a change in behavioral ecology. Rate of consumption remained constant through 17 August. Activity patterns and activity budget showed no changes indicative of lower foraging efficiency. Rates of movement

showed no seasonal trends. The home range of Fox 3 increased in size during every 10-d period, but this may be due to sampling problems rather than changes in home range use.

In summary, the caching of eggs and caribou meat provided a defendable resource through a season of low small mammal availability. In addition, arctic foxes were found to maintain a pair bond through a summer in which no successful reproduction had occurred. The members of a mated pair shared a relatively large home range and defended it from neighboring foxes and transients.

APPENDIX 1. List of plants encountered in the Demarcation Bay study area, Alaska (see Fig. 1).

Family	Species
Betulaceae	Betula nana
Boraginaceae	Eritrichium aretioides
	Mertensia maritima
Caryophyllaceae	Cerastium beeringianum
	Honckenya peploides
	Melandrium apetalum
	Minuarta arctica
	Silene acaulis
	Stellaria crassifolia
	S. edwardsii
	S. humifusa
	S. laeta
	S. longipes
Compositae	Artemisia arctica
	Chrysanthemum integrifolium
	Petasites frigidus
	Saussurea angustifolia
	Senecio atropurpureus
	S. congestus
	S. resedifolius
Crassulaceae	Sedum rosea
Cruciferae	Cardamine hyperborea
	C. pratensis
	Cochlearia officinalis
	Draba cinerea
	D. macrocarpa
	D. nivalis
	D. pseudopilosa
	Eutrema edwardsii
	Parrya nudicaulis
Cyperaceae	Carex aquatilis
	C. bigelowii
	C. gmelini
	C. mackenziei
	C. membranacea
	C. misandra
	C. petricosa
	C. rariflora
	C. rotundata

Appendix 1. (cont.)

Family	Species
Cyperaceae (cont.)	C. saxatilis
	C. subspathacea
	C. supina
	C. ursina
	Eriophorum angustifolium
	E. russeolum
	E. scheuchzeri
	E. vaginatum
Empetraceae	Empetrum nigrum
Equisetaceae	Equisetum arvense
	E. variegatum
Ericaceae	Cassiope tetragona
	Ledum palustre
	Vaccinium uliginosum
	V. vitis-idaea
Gentianaceae	Gentiana sp.
Graminae	Alopecurus alpinus
	Arctagrostis latifolia
	Arctophila fulva
	Dupontia fischeri
	Festuca baffinensis
	F. brachyphylla
	F. vivipara
	Hierochloe alpina
	H. pauciflora
	Poa arctica
	P. glauca
	P. lanata
	P. paucispicula
	Puccinellia phryganodes
	Trisetum spicatum
Haloragaceae	Hippuris tetraphylla
Juncaceae	Juncus arcticus
	J. biglumis
	J. castaneus
	Luzula arctica
	L. confusa
	L. multiflora
	L. tundricola

Appendix 1. (cont.)

Family	Species
	L. wahlenbergii
Leguminosae	Astragalus alpinus
	A. umbellatus
	Lupinus arcticus
	Oxytropis maydelliana
	O. nigrescens
Liliaceae	Lloydia serotina
Onagraceae	Epilobium latifolium
Papaveraceae	Papaver hultenii
Polemoniaceae	Polemonium acutiflorum
	P. boreale
Polygonaceae	Oxyria digyna
	Polygonum bistorta
	P. viviparum
	Rumex arctica
Primulaceae	Primula borealis
Pyrolaceae	Pyrola grandiflora
Ranunculaceae	Anenome parviflora
	Caltha palustris
	Delphinium brachycentrum
	Ranunculus gmelini
	R. nivalis
	R. pallasii
Rosaceae	Dryas integrifolia
	Potentilla hyparctica
	P. uniflora
	P. virgulata
	Rubus chamaemorus
Salicaceae	Salix arctica
	S. glauca
	S. lanata
	S. phlebophylla
	S. polaris
	S. reticulata

Appendix 1. (cont.)

Family	Species
Saxifragaceae	Boykinia richardsonii
	Chrysosplenium tetrandum
	Saxifraga caespitosa
	S. cernua
	S. foliosa
	S. hieracifolia
	S. hirculus
	S. oppositifolia
	S. punctata
Scrophulariaceae	Castilleja hyperborea
	Lagotis glauca
	Pedicularis capitata
	P. kanei
	P. langsdorfii
	P. sudetica
Valerianaceae	Valeriana capitata

APPENDIX 2. List and description of percent cover and frequency of occurrence variables used to describe vegetation types and habitat use patterns at Demarcation Bay, Alaska.

A. Percent cover variables

1. *Carex aquatilis*
2. *C. bigelowii*
3. Other rhizomatous Cyperaceae:
   - excludes: *Carex aquatilis*, *C. bigelowii*, *C. subspathacea*, *Eriophorum angustifolium*
   - includes: *Carex rariflora*, *C. membranacea*, *Juncus arcticus*, *J. biglumis*
4. *Eriophorum angustifolium*
5. *Dupontia fischeri*
6. Other rhizomatous Graminae:
   - excludes: *Dupontia fischeri*, *Poa (arctica)*
   - includes: *Hierochloe pauciflora*, *Arctophila fulva*, *Alopecurus alpinus*
7. Moss
8. Lichen
9. *Salix reticulata*
10. *S. arctica*
11. *S. phlebophylla*
12. *Poa* spp.
13. *Eriphorum vaginatum*
14. Bare ground
15. Water
16. Tufted Cyperaceae
    - includes: *Carex misandra*, *C. saxatilis*
17. Tufted Graminae
    - includes: *Festuca baffinensis*, *Hierochloe alpina*, *Arctagrostis latifolia*
18. Heath associates
    - includes: *Dryas integrifolia*, *Cassiope tetragona*, *Ledum palustre*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, *Rubus chamaemorus*
19. *Luzula* spp.
20. Saxifragaceae
21. Caryophyllaceae
22. Other (includes all herbaceous and graminoid species which rarely have percent cover values and which do not belong to the common growth form categories already listed).
    - includes: *Carex subspathacea*, *Salix lanata*, *Saussurea angustifolia*, *Silene acaulis*, *Oxytropis nigrescens*, *Cardamine pratensis*, *Cochlearea officinalis*, *Pedicularis* spp., *Oxytropis maydelliana*, *Rubus chamaemorus*, *Astragalus alpinus*, *Polygonum viviparum*

Appendix 2. (cont.)

23. Total rhizomatous Cyperaceae
includes: Carex aquatilis, C. bigelowii, C. membranacea, C. rariflora, Eriophorum angustifolium, Juncus arcticus, J. biglumis

24. Total Graminae
includes: Dupontia fischeri, Poa (arctica), Hierochloe pauciflora, H. alpina, Arctophila fulva, Alopecurus alpinus, Festuca baffinensis, Arctagrostis latifolia

25. Total Salix spp.

26. Total herbaceous

27. Total graminoid

28. Total woody
includes: Salix spp., Vaccinium vitis-idaea, Cassiope tetragona, Empetrum nigrum, Ledum palustris

B. Frequency of occurrence variables.

1. Legumes
includes: Astragalus alpinus, A. umbellatus, Oxytropis maydelliana, O. nigrescens

2. Salix spp.
includes: Salix arctica, S. reticulata, S. phlebophylla, S. lanata

3. Total herbaceous
includes: Artemisia arctica, Astragalus alpinus, Astragalus umbellatus, Caltha palustris, Cardamine hyperborea, Cardamine pratensis, Cerastium beeringianum, Chrysosplenium tetrandum, Cochlearea officinalis, Delphinium brachycentrum, Draba. spp., Equisetum spp., Eritrichium aretioides, Eutrema edwardsii, Hippuris tetraphylla, Lagotis glauca, Lloydia serontina, Melandrium apetalum, Minuarta arctica, Oxyria digyna, Oxytropis maydelliana, O. nigrescens, Papaver hultenii, Parrya nudicaulis, Pedicularis capitata, Pedicularis kanei, P. langsdorffi, P. sudetica, Petasites frigidus, Polemonium acutiflorum, Polemonium boreale, Polygonum bistorta, Polygonum viviparum, Primula borealis, Pyrola grandiflora, Ranunculus gmelini, Ranunculus nivalis, R. pallasii, Rubus chamaemorus, Saussurea angustifolia, Saxifraga caespitosa, Saxifraga cernua

Appendix 2. (cont.)

	S. foliosa	S. hieracifolia
	S. hirculus	S. oppositifolia
	S. punctata	Sedum rosea
	Senecio atropurpureus	Silene acaulis
	Stellaria crassifolia	S. longipes
	Valeriana capitata	
4. Total graminoid		
includes:	Alopecurus alpinus	Arctogrostis latifolia
	Arctophila fulva	Carex aquatilis
	Carex bigelowii	C. membranacea
	C. misandra	C. rariflora
	C. saxatilis	C. subspathacea
	C. ursina	Dupontia fischeri
	Eriophorum angustifolium	Eriophorum russeolum
	E. scheuchzeri	E. vaginatum
	Festuca spp.	Hierochloe alpina
	Hierochloe pauciflora	Juncus arcticus
	Juncus biglumis	Juncus castaneus
	Luzula arctica	Luzula confusa
	L. multiflora	L. tundricola
	L. wahlenbergii	Poa spp.
	Puccinellia phryganodes	Trisetum spicatum
	Unknown graminae	
5. Total Saxifragaceae		
includes:	Chrysosplenium tetrandum	Saxifraga caespitosa
	Saxifraga cernua	S. foliosa
	S. hieracifolia	S. hirculus
	S. oppositifolia	S. punctata
6. Total heath		
includes:	Cassiope tetragona	Dryas integrifolia
	Empetrum nigrum	Ledum palustre
	Pyrola grandiflora	Vaccinium uliginosum
	Vaccinium vitis-idaea	Rubus chamaemorus
7. Total Graminae		
includes:	Alopecurus alpinus	Arctagrostis latifolia
	Arctophila fulva	Dupontia fischeri
	Festuca spp.	Hierochloe alpina
	Hierochloe pauciflora	Poa spp.
	Puccinellia phryganodes	Trisetum spicatum
	Unknown Graminae	
8. Total Cyperaceae and Juncaceae		
includes:	Carex aquatilis	C. bigelowii
	C. membranacea	C. misandra
	C. rariflora	C. saxatilis
	C. subspathacea	C. ursina
	Eriophorum angustifolium	Eriophorum russeolum
	E. scheuchzeri	E. vaginatum

Appendix 2. (cont.)

	Juncus arcticus	Juncus biglumis
	J. castaneus	Luzula arctica
	Luzula confusa	L. multiflora
	L. tundricola	L. wahlenbergii
9. Total Cruciferae		
includes:	Cardamine hyperborea	C. pratensis
	Cochlearea officinalis	Draba spp.
	Eutrema edwardsii	Parrya nudicaulis
10. Total woody		
includes:	Empetrum nigrum	Cassiope tetragona
	Ledum palustre	Vaccinium vitis-idaea
	Salix arctica	Salix lanata
	S. phlebophylla	S. reticulata

APPENDIX 3. Proportion of 1-m^2 plots sampled in which each plant species encountered was present in each vegetation type on the 30-ha study plot at Demarcation Bay, Alaska.

Species	Habitat types														
	TOTAL	CM	DM	DCM	LR	MR	HR	TS	HCP	AM	TER	FB	DT	ST	CP
Total	1.000	0.035	0.062	0.120	0.132	0.103	0.038	0.048	0.135	0.006	0.084	0.049	0.102	0.074	0.009
Alopecurus alpinus	0.014	0.	0.063	0.	0.	0.	0.276	0.	0.	0.	0.	0.	0.	0.	0.
Arctagrostis latifolia	0.074	0.	0.	0.032	0.098	0.013	0.034	0.243	0.192	0.	0.031	0.158	0.013	0.070	0.
Arctophila fulva	0.031	0.111	0.021	0.	0.	0.025	0.	0.	0.010	0.800	0.	0.	0.152	0.018	0.
Artemisia arctica	0.004	0.	0.	0.	0.	0.	0.034	0.027	0.	0.	0.	0.	0.013	0.	0.
Astragalus alpinus	0.003	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.053	0.	0.	0.
A. umbellatus	0.004	0.	0.	0.	0.	0.	0.	0.	0.010	0.	0.	0.053	0.	0.	0.
Caltha palustris	0.010	0.185	0.	0.	0.010	0.	0.	0.	0.	0.200	0.	0.	0.013	0.	0.
Cardamine hyperborea	0.098	0.037	0.	0.086	0.020	0.125	0.034	0.216	0.240	0.	0.077	0.237	0.038	0.070	0.
C. pratensis	0.116	0.074	0.083	0.	0.020	0.050	0.034	0.351	0.308	0.200	0.062	0.158	0.165	0.140	0.
Carex aquatilis	0.758	1.000	0.313	0.968	0.902	0.875	0.931	0.378	0.385	0.600	0.908	0.737	0.886	0.807	0.714
C. bigelowii	0.175	0.	0.021	0.054	0.059	0.038	0.069	0.676	0.567	0.	0.108	0.368	0.051	0.158	0.
C. membranacea	0.009	0.	0.	0.022	0.029	0.	0.	0.	0.	0.	0.015	0.	0.013	0.	0.
C. misandra	0.023	0.	0.	0.011	0.010	0.025	0.	0.	0.	0.	0.092	0.	0.025	0.105	0.
C. rariflora	0.062	0.037	0.125	0.043	0.049	0.100	0.	0.054	0.010	0.	0.154	0.132	0.	0.088	0.143
C. saxatilis	0.025	0.	0.	0.054	0.020	0.013	0.138	0.	0.019	0.	0.031	0.	0.025	0.018	0.
C. subspathacea	0.012	0.	0.063	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.857
C. ursina	0.003	0.	0.042	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
Cassiope tetragona	0.022	0.	0.	0.043	0.010	0.038	0.034	0.027	0.010	0.	0.077	0.026	0.	0.	0.
Cerastium beeringianum	0.049	0.037	0.188	0.	0.010	0.038	0.	0.	0.010	0.	0.	0.	0.241	0.053	0.143
Chrysosplenium tetrandum	0.089	0.	0.688	0.011	0.029	0.138	0.	0.027	0.048	0.	0.092	0.053	0.063	0.018	0.143
Cochlearia officinalis	0.074	0.037	0.563	0.	0.020	0.050	0.	0.	0.	0.	0.	0.	0.253	0.018	0.286
Draba spp.	0.167	0.185	0.271	0.086	0.049	0.138	0.	0.297	0.163	0.	0.169	0.132	0.367	0.228	0.143
Dryas integrifolia	0.400	0.222	0.021	0.473	0.529	0.113	0.345	0.892	0.462	0.	0.631	0.895	0.076	0.386	0.143
Dupontia fischeri	0.184	0.148	0.938	0.065	0.147	0.338	0.207	0.054	0.087	0.	0.138	0.105	0.101	0.070	0.429
Empetrum nigrum	0.017	0.	0.	0.022	0.	0.025	0.276	0.	0.	0.	0.	0.	0.	0.	0.143
Equisetum spp.	0.082	0.037	0.021	0.129	0.147	0.025	0.	0.054	0.019	0.	0.092	0.474	0.025	0.035	0.
Eriophorum angustifolium	0.188	0.111	0.583	0.140	0.098	0.288	0.138	0.027	0.029	0.200	0.046	0.105	0.430	0.298	0.143
E. russeolum	0.027	0.074	0.	0.022	0.	0.013	0.034	0.	0.010	0.	0.015	0.	0.152	0.018	0.
E. scheuchzeri	0.004	0.	0.042	0.	0.	0.	0.	0.	0.	0.	0.015	0.	0.	0.	0.
E. vaginatum	0.132	0.	0.	0.	0.029	0.038	0.034	0.595	0.529	0.	0.031	0.211	0.013	0.123	0.
Eritrichium aretioides	0.001	0.	0.	0.	0.	0.	0.	0.	0.010	0.	0.	0.	0.	0.	0.
Eutrema edwardsii	0.043	0.	0.021	0.	0.	0.	0.172	0.135	0.125	0.	0.	0.132	0.013	0.053	0.
Festuca spp.	0.018	0.	0.063	0.	0.010	0.013	0.	0.027	0.019	0.	0.015	0.026	0.051	0.	0.
Hierochloe alpina	0.004	0.	0.	0.	0.010	0.013	0.034	0.	0.	0.	0.	0.	0.	0.	0.
H. pauciflora	0.048	0.	0.021	0.086	0.029	0.125	0.034	0.	0.029	0.	0.046	0.	0.038	0.088	0.
Hippuris tetraphylla	0.003	0.	0.042	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
Juncus arcticus	0.039	0.037	0.021	0.022	0.020	0.038	0.034	0.	0.	0.	0.046	0.	0.165	0.070	0.
J. biglumis	0.066	0.037	0.021	0.043	0.020	0.038	0.069	0.027	0.	0.	0.015	0.026	0.316	0.175	0.
J. castaneus	0.001	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.013	0.	0.
Lagoris glauca	0.039	0.	0.	0.	0.	0.	0.	0.270	0.096	0.	0.031	0.132	0.	0.053	0.

Appendix 3. (cont.)

Species	Habitat types														
	TOTAL	CM	DM	DCM	LR	MR	HR	TS	HCP	AM	TER	FE	DT	ST	CP
Ledum palustre	0.008	0.	0.	0.022	0.	0.	0.034	0.	0.019	0.	0.015	0.	0.	0.	0.
Luzula arctica	0.003	0.	0.	0.	0.	0.	0.034	0.	0.010	0.	0.	0.	0.	0.	0.
L. confusa	0.021	0.	0.021	0.	0.	0.038	0.034	0.027	0.087	0.	0.	0.	0.013	0.	0.
L. multiflora	0.145	0.	0.021	0.043	0.010	0.100	0.276	0.351	0.240	0.	0.031	0.132	0.392	0.246	0.
Melandrium apetalum	0.137	0.148	0.625	0.043	0.029	0.163	0.	0.027	0.	0.	0.077	0.	0.342	0.298	0.286
Minuarta arctica	0.003	0.	0.	0.	0.	0.	0.	0.027	0.	0.	0.	0.026	0.	0.	0.
Oxyria digyna	0.005	0.	0.	0.	0.020	0.013	0.034	0.	0.	0.	0.	0.	0.	0.	0.
Oxytropis maydelliana	0.019	0.	0.	0.	0.	0.	0.	0.108	0.077	0.	0.	0.053	0.	0.018	0.
O. nigrescens	0.004	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.079	0.	0.	0.
Papaver nultenii	0.018	0.	0.	0.011	0.020	0.013	0.	0.135	0.019	0.	0.015	0.053	0.	0.	0.
Parrya nudicaulis	0.001	0.	0.	0.	0.	0.	0.	0.027	0.	0.	0.	0.	0.	0.	0.
Pedicularis capitata	0.096	0.	0.	0.043	0.059	0.063	0.034	0.243	0.346	0.	0.062	0.158	0.	0.053	0.
P. kaneii	0.006	0.	0.	0.032	0.010	0.	0.	0.	0.	0.	0.	0.026	0.	0.	0.
P. langsdorfii	0.035	0.	0.	0.022	0.029	0.063	0.	0.027	0.067	0.	0.062	0.026	0.025	0.018	0.143
P. sudetica	0.047	0.	0.	0.032	0.078	0.063	0.069	0.027	0.067	0.	0.015	0.158	0.	0.018	0.286
Pedicularis spp.	0.515	0.333	0.104	0.634	0.637	0.450	0.517	0.649	0.442	0.	0.692	0.605	0.405	0.667	0.143
Petasites frigidus	0.019	0.	0.	0.	0.010	0.025	0.069	0.054	0.048	0.	0.015	0.053	0.	0.	0.
Poa spp.	0.225	0.074	0.271	0.043	0.088	0.300	0.379	0.243	0.365	0.	0.123	0.316	0.443	0.140	0.143
Polemonium acutiflorum	0.013	0.	0.	0.011	0.	0.038	0.034	0.	0.029	0.	0.	0.053	0.	0.	0.
P. boreale	0.001	0.	0.	0.	0.	0.	0.	0.	0.010	0.	0.	0.	0.	0.	0.
Polygonum bistorta	0.052	0.	0.021	0.011	0.010	0.	0.	0.405	0.144	0.	0.077	0.	0.	0.035	0.
P. viviparum	0.668	0.259	0.167	0.624	0.627	0.700	0.690	0.784	0.827	0.	0.831	0.868	0.671	0.825	0.143
Potentilla spp.	0.013	0.	0.	0.	0.	0.013	0.207	0.027	0.019	0.	0.	0.	0.	01	01
Pyrola grandiflora	0.001	0.	0.	0.	0.	0.	0.	0.027	0.	0.	0.	0.	0.	0.	0.
Ranunculus gmelini	0.004	0.	0.	0.	0.	0.	0.	0.	0.	0.200	0.	0.	0.025	0.	0.
R. nivalis	0.004	0.	0.042	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.143
R. pallassii	0.014	0.037	0.063	0.	0.	0.013	0.	0.	0.	0.200	0.	0.	0.063	0.	0.
Rubus chamaemorus	0.043	0.	0.	0.	0.020	0.025	0.034	0.027	0.048	0.	0.262	0.079	0.	0.035	0.
Salix arctica	0.809	0.481	0.313	0.914	0.882	0.813	0.828	0.838	0.952	0.200	0.815	0.974	0.734	0.930	0.143
S. lanata	0.025	0.	0.	0.108	0.	0.025	0.069	0.027	0.019	0.	0.	0.	0.013	0.018	0.
S. phlebophylla	0.149	0.	0.	0.043	0.020	0.088	0.483	0.351	0.529	0.	0.108	0.132	0.051	0.070	0.
S. reticulata	0.582	0.259	0.021	0.495	0.676	0.450	0.793	1.000	0.885	0.200	0.800	0.895	0.253	0.544	0.143
Saussurea angustifolia	0.075	0.	0.	0.	0.	0.013	0.034	0.378	0.308	0.	0.046	0.053	0.	0.088	0.
Saxifraga caespitosa	0.001	0.	0.	0.	0.	0.	0.	0.	0.010	0.	0.	0.	0.	0.	0.
S. cernua	0.374	0.407	0.958	0.258	0.147	0.500	0.138	0.189	0.288	0.200	0.200	0.211	0.785	0.439	0.429
S. foliosa	0.048	0.	0.063	0.032	0.029	0.088	0.069	0.	0.	0.	0.062	0.	0.114	0.105	0.
S. hieracifolia	0.013	0.037	0.	0.	0.	0.013	0.034	0.	0.038	0.	0.	0.053	0.	0.018	0.
S. hirculus	0.457	0.296	0.292	0.452	0.402	0.413	0.172	0.405	0.308	0.	0.646	0.684	0.608	0.789	0.286
S. oppositifolia	0.004	0.	0.	0.022	0.	0.	0.034	0.	0.	0.	0.	0.	0.	0.	0.
S. punctata	0.018	0.	0.	0.022	0.	0.	0.034	0.162	0.029	0.	0.	0.	0.	0.035	0.
Senecio atropurpureus	0.083	0.037	0.	0.022	0.	0.038	0.069	0.297	0.269	0.	0.031	0.316	0.	0.053	0.
Silene acaulis	0.025	0.	0.	0.011	0.	0.	0.103	0.054	0.058	0.	0.046	0.079	0.	0.018	0.
Stellaria crassifolia	0.044	0.037	0.479	0.	0.	0.063	0.	0.027	0.	0.	0.	0.	0.025	0.	0.286
S. longipes	0.486	0.259	0.438	0.280	0.255	0.475	0.483	0.784	0.798	0.	0.462	0.632	0.595	0.509	0.286
Trisetum spicatum	0.008	0.	0.021	0.	0.010	0.013	0.069	0.	0.	0.	0.015	0.	0.	0.	0.

Appendix 3. (cont.)

Species	Habitat types														
	TOTAL	CM	DM	DCM	LR	MR	HR	TS	HCP	AM	TER	FB	DT	ST	CP
Vaccinium uliginosum	0.001	0.	0.	0.	0.	0.	0.034	0.	0.	0.	0.	0.	0.	0.	0.
V. vitis-idaea	0.107	0.	0.	0.065	0.010	0.225	0.552	0.081	0.308	0.	0.077	0.	0.	0.035	0.
Valeriana capitata	0.001	0.	0.	0.	0.	0.	0.034	0.	0.	0.	0.	0.	0.	0.	0.
Moss	0.908	0.815	0.542	0.968	0.951	0.825	0.931	1.000	1.000	0.400	0.938	0.974	0.937	0.947	0.714
Lichen	0.600	0.148	0.	0.527	0.578	0.638	0.897	0.946	0.923	0.	0.769	0.842	0.532	0.333	0.143
Unidentified Graminae	0.087	0.037	0.021	0.065	0.078	0.013	0.034	0.054	0.221	0.	0.169	0.079	0.051	0.070	0.286

Appendix 4. Methods and data used for calculating average litter size and age at first capture of small mammals.

A. Average litter sizes

The average litter size of L. sibericus has been reported as 7.0 (range 1 to 13) (Mullen 1968), 7.3 (Barkalow 1952), 3.7 (Sutton and Hamilton 1932, from Barkalow 1952), 4.4 (Rausch and Rausch 1975) and 7.1 to 7.6 (Batzli et al. 1974). For D. torquatus, Manning (1954) reported an average litter size of 5.47. M. oeconomus average litter sizes have been reported as 6.7 (Kostian 1970) and 7.2 (Tast 1966). In this study, data from trap deaths of pregnant females give an average litter of 5.8 (n=4) for M. oeconomus, 2 (n=1) for D. torquatus, and 6 (n=1) for L. sibericus. A conservative litter size of 5 was used in Table 7 to estimate the number of births for all species.

B. Age at first capture

Growth rate equations of Collier et al. (1975) for L. sibericus were used to estimate the age of animals which entered the trappable population at a weight less than 40 g. Collier et al.'s equations are:

suckling weight (age 0 to 15)= 0.64A + 3.3

weanling weight (age 16 to 28)= A - 2.1

adult weight (over 28 days) = $a\ (1\text{-}ce^{-bA})$

where A=age in days, a is an asymptote approached by adult weight, and

Appendix 4. (cont.)

the constants b and c are chosen so that at age 28 d adult weight= 25.9 g and dW/dA= 1 g/d. Then (also from Collier et al. 1975):

for females, adult weight= $132\ (1 - 1.05e^{-0.0094A})$,

for males, adult weight= $102\ (1 - 1.08e^{-0.013A})$.

Animals weighing more than 40 g at first capture were eliminated from this analysis for 2 reasons: 1) the growth rate equations are only an approximation to growth under optimal conditions, being quite variable in natural conditions and more a criterion of physiological than chronological age (Krebs 1964); and 2) adults weighing more than 40 g at first capture may not have originated on the study plot.

Solving these growth rate equations for age introduces some error to the estimate because captured animals could not be identified as suckling, weanling, or adult with certainty. However, this was of little consequence as age was used to assign birth to a 10-d to 14-d period.

APPENDIX 5. Common and scientific names of birds present at Demarcation Bay, Alaska, in the summers of 1978 and 1979. Species which where confirmed breeders in either year are marked with an asterisk (*).

Common names	Scientific names
Yellow-billed loon	Gavia adamsii
* Red-throated loon	Gavia stellata
* Arctic loon	Gavia arctica
* Tundra swan	Cygnus columbianus
White-fronted goose	Anser albifrons
Snow goose	Chen caerulescens
Brant	Branta bernicla
Canada goose	Branta canadensis
* Green-winged teal	Anas crecca
Mallard	Anas platyrhynchos
Northern pintail	Anas acuta
Northern shoveler	Anas clypeata
American widgeon	Anas americana
Greater scaup	Aythya marila
* Common eider	Somateria mollissima
King eider	Somateria spectabilis
Spectacled eider	Somateria fischeri
* Oldsquaw	Clangula hyemalis
Common scoter	Oedemia nigra
Surf scoter	Melanitta perspicillata
White-winged scoter	Melanitta deglandi
* Red-breasted merganser	Mergus serrator
Northern harrier	Circus cyaneus
Rough-legged hawk	Buteo lagopus
Golden eagle	Aquila chrysaetos
Gyrfalcon	Falco rusticolus
Peregrine falcon	Falco peregrinus
Merlin	Falco columbarius
* Willow ptarmigan	Lagopus lagopus
* Rock ptarmigan	Lagopus mutus
* Sandhill crane	Grus canadensis
* Lesser golden-plover	Pluvialis dominica
Black-bellied plover	Pluvialis squatarola
Semipalmated plover	Charadrius semipalmatus
Whimbrel	Numenius phaopus
Ruddy turnstone	Arenaria interpres
Sanderling	Calidris alba
* Semipalmated sandpiper	Calidris pusillus
* Baird's sandpiper	Calidris bairdii
* Pectoral sandpiper	Calidris melanotos
Dunlin	Calidris alpina
* Stilt sandpiper	Micropalama himantopus

Appendix 5. (cont.)

Common names	Scientific names
* Buff-breasted sandpiper	Tryngites subruficollis
Long-billed dowitcher	Limnodromus scolopaceus
* Red-necked phalarope	Phalaropus lobatus
* Red phalarope	Phalaropus fulicaria
Common snipe	Gallinago gallinago
Pomerine jaeger	Stercorarius pomerinus
* Parasitic jaeger	Stercorarius parasiticus
* Long-tailed jaeger	Stercorarius longicaudus
Herring gull	Larus argentatus
* Glaucous gull	Larus hyperboreus
Sabines' gull	Xema sabini
* Arctic tern	Sterna paradisaea
Snowy owl	Nyctea scandiaca
Short-eared owl	Asio flammeus
Barn swallow	Hirundo rustica
Cliff swallow	Petrochelidon pyrrhonota
Violet-green swallow	Tachycineta thalassina
Common raven	Corvus corax
Varied thrush	Ixoreus naevius
Rusty blackbird	Euphagus carolinus
Savannah sparrow	Passerculus sandwichensis
White-crowned sparrow	Zonotrichia leucophrys
* Lapland longspur	Calcarius lapponicus
* Snow bunting	Plectrophenax nivalis
Redpoll	Carduelis flammea

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